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THE EVOLUTION OF THE ANGIOSPERMS; HISTORICAL AND ECOLOGICAL EVIDENCE

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In my presidential addresses and other papers on the evolution of the flowering plants (Thomas, 1936, 1938, 1957, 1958) I held that we should look to the fossils to learn about the genetic relationships of the angiosperms. Idealistic morphology and the *urform* have their place in plant morphology but the *urform* is not be confused with the ancestor.

As time has gone on we have tried to find angiosperm ancestors in several different plant groups, the Ferns, the Cycads, the Conifers and Gnetales ; and later, with the advances in our knowledge of fossil botany, in the Bennettitales ; however, all of these seem too different from angiosperms. But in the great but loose group of the Pteridosperms that flourished widely in the upper Palaeozoic and older Mesozoic there seems hope. These plants disappeared at about the time the angiosperms arose to dominance. Of recent years our information about the fossil angiosperms from the time of their rise to dominance in the Middle Cretaceous has grown and we can speak more confidently about the early flowering plants. Our information from fossil leaves has been supplemented with information from fossil fruits and latterly from pollen. Very often these fossil remains can be referred to living genera.

The species found in the fossil flora of a region vary with the passage of time, and this variation seems to be due to changes in climate. Climatic fluctuations took place during the Quaternary and Tertiary periods, and very probably at earlier times. The studies that have been made on the more recent fossil floras show that climatic change generally brought about migration of the flora into areas where the ecological conditions were those required by the principal species. At a later period there may have been a return to the former conditions and a re-establishment of the old type of vegetation in the areas it formerly occupied.

It is remarkable that very little morphological change seems to have occurred during such migrations. It seems highly probable that the climatic changes which affected the vegetation were not merely local in operation but affected the whole of the world. The changes in temperature and rainfall which caused the great Quaternary extension of the arctic ice, acted in the same way in Europe, in North America and probably in Northern Asia. The same factors were also responsible for a pluvial period in Central Africa and the Middle East, of which remarkable evidence exists. The considerations put forward by Sir George Simpson (1939) based on purely physical and meterological principles are of the highest importance in relation to former changes in climates. Before the Quaternary glaciations the Pliocene vegetation of both Europe and North America was generally similar to that of Post-glacial times. Thus 87 per cent of the genera recognizable in the Teglen flora still occur in Western Europe, though in addition there were a few forms which are now extinct in Europe but occur in North America and China. The evidence from the present distribution of species in circumpolar regions and also from Pliocene fossils, suggests that the floras of Europe, North America and Eastern Asia were formerly closely similar in composition. The Pleistocene glaciation brought about a general southward retreat of the vascular plants from the Arctic. In China and America there were mountain ranges running north and south, forming corridors by which species could travel southwards and return when the climate became once more suitable. Europe is different. Southward paths were blocked by the Mediterranean Sea and by the East-West running mountain ranges. For this reason some species were exterminated and never returned to their old habitats when the amelioration of the climate took place.

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[1] Dr. Hamshaw Thomas intended to give this paper as his address at the conclusion of his last year of office as President of the Society ; he was prevented from doing so by indisposition.

Several great fossil floras of the Tertiary period are known in West Europe. Thus Heer (1856–1859) studied the old lake deposits at Oeningen in Switzerland and distinguished 739 species of leaves, fruits and flowers, belonging to 89 angiosperm families. No doubt his work needs to be revised, but later workers like Clement Reid have reached conclusions similar in kind and we feel fairly sure that a similar rich flora occurred in Europe and N. America.

There are great deposits of decayed Tertiary plants, often 30 ft thick, forming the Brown coal, and found in small basins across Europe from Holland to Turkey. They indicate a very rich and luxuriant vegetation, much of it angiospermous. Then the pyritized fruits and seeds of Southern England of the London Clay are of great interest. Mrs Reid and Miss Chandler described 314 species referable to 100 genera in 1933 and there are many more. Most belong to genera of woody plants of the lowland Tropics.

The Tertiary floras of N. America form a continuous series and some are very rich.

E. W. Berry (1937) studied the Wilcox (Lower Eocene) Plants and recognized 500–600 species which he referred to 180 genera. A remarkably large number of localities on the Pacific side of the continent have yielded floras of different sizes which have received careful study from Prof. R. W. Chaney (1944) and his pupils. Working with large numbers of specimens, they found that the fossils could often be very closely compared with leaves of forms still living near the Pacific coast, either in the U.S.A. or in Mexico or Central America. The identifications made of the specimens are very reliable.

The numbers of Dicotyledons and their variety is indicated by the following examples :—

Chalk Bluffs, Middle Eocene of Sierra Nevada.
  74 species, 63 genera, 41 families.
    (MacGinitie 1941.)
La Porte, California. Upper Eocene.
  41 species, 34 genera, 24 families.
    (Potbury, S.S. 1935.)
Goshen, Eocene or Oligocene, of Oregon.
  49 species, 32 genera, 28 families.
    (Chaney & Sandborn, 1933.).
Florissant. Lower Oligocene of Colorado.
  100 species, 77 genera, 39 families.
    (MacGinitie, H. D. 1953.)
Mascal, Miocene of Columbia Plateau.
  76 species, 34 genera, 23 families.
    (Chaney & Axelrod 1959.)
Mulholland. Pliocene of California.
  41 species, 28 genera, 17 families.
    (Axelrod, D. I. 1944.)

Tertiary plant remains are found in many parts of temperate Asia. They represent, for the most part, associations of summer-green (temperate) forest plants. Many of the genera present were the same as those occurring at the same period in Europe and America. The fossil floras of South-East Asia are, however, rather sparse and not unlike some of the floras still living in the region.

In the Upper Cretaceous rocks, there are some great floras with angiosperms, particularly in the Arctic. There are fine specimens from Alaska and Disco Is. in West Greenland. Some forty families of dicotyledons have been identified, many of them the same as in the Tertiary rocks. Some of the determination may need revision but the presence of the following families seems to be well established :—

> Aceraceae, Annonaceae, Lauraceae, Magnoliaceae, Platanaceae, Leguminosae, Myrtaceae, Moraceae, Salicaceae, Betulaceae, and Euphorbiaceae. The Monocotyledons are represented by the leaves and stems of Palms, and in several places by specimens resembling parts of plants of Cyperaceae or Typhaceae.

Most of these families are also known from Cretaceous floras further south, and there is now no reason to suppose that the angiosperms first arose in the Arctic. I am sure the angiosperms must have arisen long before the Upper Cretaceous period.

The long series of plant remains from the Cretaceous to the present day might be expected to furnish some clear indications of evolutionary trends in the Angiosperms. Comparison of the form and structure in examples of different ages referable to the same family should show changes in structure indicating evolutionary progression. But although a considerable quantity of material must exist which could be studied in this way, little has been published about the results of such investigations. Miss Chandler (1923) has given an interesting account of the evolutionary changes which have occurred in the fruits and seeds of the genus *Stratiotes* from the Upper Eocene to the present. She found that there was considerable morphological similarity between all the known forms although there were differences in detail or micro structure. Many fruits and seeds which occur in the early Tertiary rocks, appear in an almost identical form and structure today. In the same way many Tertiary and Recent leaves are identical in outline, size, main veins and minor venation. It seems probable that morphological changes have been extremely slow, and in some genera there have been no changes at all over a very long period.

By the study of as many genera as possible, whose ancestors can be traced back to Eocene times, we should obtain at least some idea of floral evolution. For example, of about 40 families in the Eocene, only eight have genera with sympetalous flowers, but in a modern tropical flora, such as that of Africa, half the families include sympetalous flowers. This does indicate the direction of evolution. Then also most of the Eocene Angiosperms were woody. Of 31 families from the Eocene of Western America, 20 are not only woody, but have characters which the wood anatomists consider primitive.

Some of the evolutionary conclusions from the study of the Eocene flora are contrary to a good deal of current morphological theory. Thus few of the London Clay genera, in fact Magnolia alone, have the supposedly primitive elongated receptacle and spirally inserted parts. Instead they have a disc or cup-shaped receptacle. We must admit on the other hand we see no clue on the evolution of leaf form for the Eocene trees show much the same range as the trees of today.

The question whether woodiness is primitive in angiosperms was once debated and was reviewed by Agnes Arber in 1928 and by Dr H. Bancroft in 1930.

Herbaceous families were very poorly represented in the Eocene floras.

Some have argued that the remains of herbaceous dicotyledons are likely to be under-represented as fossils, either because their leaves were unsuited to being preserved, or because they make a very small part of the vegetation of dense forest. It is noteworthy that Dr Sporne's statistical work indicates that herbaceous families are on the whole more advanced than woody ones.

Assuming that we are now acquainted with reasonable samples of the vegetation of the Northern Hemisphere from Upper Cretaceous times to the present day, it would seem certain that the processes of evolutionary change have been very slow and therefore that the ancestors of the flowering plants are likely to have been widespread at an earlier period and perhaps by the close of the Palaeozoic. I suggested some time ago that certain of the essential features of the angiosperms were to be found among the Pteridosperms of Carboniferous times.

Most Pteridosperms had large very much divided leaves, but some of the later ones had less divided leaves with reticulate venation. Their reproductive organs were much branched and they have several features in common with stamens. The pteridosperm seeds whose structure is known to us, show some major biological similarities to angiosperm seeds, as well as some differences. It is true that we know no form transitional between a Carboniferus pteridosperm and a modern angiosperm. This may be because we know so little of the Permian and Triassic fossils. Or of course we may have a wrong idea of what to look for.

Prof. D. I. Axelrod (1952) has put forward a view which seems to clear up much of this difficulty in a very satisfactory manner and which I consider is most probably correct. He has pointed out that most of the plants whose remains are found in the Carboniferous and Permain rocks are representatives of marsh vegetation and are shown by geological and anatomical evidence to have grown in swamps or estuaries. The structure of many of their dominant forms when studied from a physiological and ecological view-point shows that they could not have grown on dry land or in a well drained habitat. We know little of the plants which at this period grew on the uplands which must have been covered with vegetation. There are, however, among the remains of the marsh forms a few species with distinct structure which may well represent the remains of the stems of upland plants that had been washed down by rivers into the marshes, and after a considerable amount of decay, incorporated with the remains which were petrified in coal-balls. Writers on palaeobotany have often tended to emphasize the similarity of the fossil floras found in different parts of the world dating from about the same period, but it should be remembered that there are also considerable differences in the species associated to form the flora in different places. In certain instances the contemporary floras of diverse regions are widely different, both in the dominant genera and in the less common species associated with them. The most striking example of this is furnished by the Glossopteris floras of the Southern Hemisphere when compared with the Eurasian floras of late Palaeozoic and Early Mesozoic times. Comparatively little mixing of the species from the two floras occurs, and critical examination of some of genera, like the Pteridosperms formerly known as Thinnfeldia, and supposed to occur in both the Eurasian and the Gondwana floras, has shown that considerable differences at least of generic value exist between the northern and southern species. Thus there are no reasons which render improbable the existence at the same period in some places of vegetation containing early angiosperms while such vegetation was absent elsewhere.

Axelrod believes that the upland areas inhabited by the early angiosperms were most probably situated in the Tropics and brings forward evidence from the present geographical distribution of the families of flowering-plants in support of this view.

This, however, raises the question : where were the Tropics situated when the angiosperms rose to dominance ? We know of the former existence of immense ice-sheets covering most of the southern part of Africa and probably extending near to the present Equator. Glacial deposits and other evidence of glaciers of great size are found in India, Australia and South America. Recent observations on palaeomagnetism also indicate that about the end of the Palaeozoic period the equator and the poles occupied positions considerably different from those they have today and this must have involved a different distribution of rainfall. We know enough to convince us that many great changes of climate occurred between the Carboniferous and today these must have caused plant migration or extinction and very possibly have affected plant evolution.

The plants which have undergone very little change since the Cretaceous or early Tertiary periods are clearly a conservative element in our flora. Perhaps genera which are unknown in those floras are of recent evolution, and may be genetically unstable.

Great, but local, changes of climate must have been caused by mountain building which contributed to the evolution of the endemic species of the Alps, Himalayas and other high mountains. Possibly indeed the increased cosmic ray incidence on high mountains contributed to the appearance of new species (Thomas, 1935).

The mountain building and consequent changes in rainfall and climate must have had considerable effect on the floras of the whole world, especially during Miocene and Pliocene times. Prof. Chaney considers that the floral differentiations seen during those periods was mainly due to such changes. In both Europe and North America the floras of these periods tend to show considerable similarity to those of the Quaternary and of the present day. Thanks to the most important researches of Prof. H. Godwin (1956) and his students we now know much about the later geological history of the British Floras with the appearance and disappearance of many of the species in the glacial and interglacial periods.

There must have been related changes of climate in the southern Hemisphere. Indeed the little we know of the southern Quaternary floras indicates great alterations during these periods, and in Africa too there are signs of great migrations in the North–South direction, some of them rather recent. Plants which had migrated in a N.–S. direction would find themselves in regions of unfamiliar day length and this may have caused mutation (Heslop-Harrison & Woods, 1959).

The problems of plant evolution now involve a much wider range of study than formerly. We need a good knowledge of the earth-history of the Tertiary and Quaternary times, and of the exact dating of fossiliferous deposits by using radioactive substances ; the present state of knowledge concerning past climates and climatic change must also be taken into account. A wide knowledge of ecology and of experimental taxonomy might well indicate the general direction of change that would be induced by series of climatic variations.

Any facts which seem to show what has been the actual history of the flowering plants must be carefully scrutinized, not only for its own sake but also because of its probable influence on the philosophical basis of a large part of botanical thought. Much of the earlier speculation about angiosperm evolution has been based on the flower and much of this was dominated by views of idealistic morphology which are unrelated to evolutionary morphology. Indeed we need to scrutinize the whole of our angiosperm morphology, for much of it is based merely on traditional teaching and not on objective evidence. It seems possible that the actual evolutionary history of the flowering plants is not such a difficult problem as was formerly thought.

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SOME ASPECTS OF PALAEO-ECOLOGY IN THE KARROO OF RHODESIA AND NYASALAND

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[Summary of a paper read to the Society on 19 March 1959]

Karroo deposits occur in five main regions of the Central African Federation ; namely, the Sabi-Limpopo area in the south-east of Southern Rhodesia, the Middle Zambezi area between the plateaux of Southern and Northern Rhodesia, the Luangwa area of Northern Rhodesia, the Lower Shire area in south-west Nyasaland and the Northern Nyasaland area. Only the better known Middle Zambezi and Lower Shire areas are considered here. They are joined by Upper Karroo deposits of the Lower Zambezi area in Portuguese East Africa, a link which was perhaps present even in Lower Karroo time near the Kariba region of the present Zambezi Valley (Bond, *Trans. Geol. Soc. S. Afr.* LVIII ; 71–99, 1955).

The stratigraphical succession begins with Dwyka glacial deposits, now recognised in both Southern and Northern Rhodesia (Bond, *Trans. Geol. Soc. S. Afr.* LV, 1–12, 1953 ; Tavener-Smith, *Records Geol. Surv. N. Rhod. for 1955* (1957), 19-22). These are followed by four cycles of coarse sediments succeeded by fine, and the succession ends with extensive basaltic lavas, some of which show intercalated fossil wind-blown sand dunes. The full sequence is given in Table I where the figures (1) to (4) indicate the sedimentary cycles.

Table I.

Upper Karroo	Basalt lavas, with intercalated sediments	Jurassic
	(4) Pebbly Arkose and Forest Sandstone	Upper Triassic
	(3) Escarpment Grit and Marly Sandstone	
	················ Unconformity ················	
Lower Karroo	(2) Upper Wankie Sandstone and Madumabisa Shales	Permian
	(1) Lower Wankie Sandstone and Wankie Coal and Black Shales	
	Dwyka glacial boulder beds and varved clays	Upper Carboniferous

The Madumabisa Shales contain both bedded freshwater and concretionary limestones, while the Forest Sandstone is a wind-blown sand in its upper part.

Except for the absence of Lower Triassic beds, the succession is very similar to that in the Union of South Africa. It extends from the Upper Carboniferous to the Jurassic and, during the immense length of time covered, a major climatic change from glacial to desert conditions took place.

No fossils are yet known from the Dwyka beds, while the Lower Wankie Sandstone, Wankie Coal and Black Shales have yielded only scarce fossil plants. The Upper Wankie Sandstone, however, has a rich *Glossopteris-Gangamopteris* flora with an admixture of Northern hemisphere Upper Carboniferous and Permian species. The *Glossopteris* flora persists into the Madumabisa Shales, but

Gangamopteris is absent. New arrivals include Taeniopterids, cycadophyte-like cones, and much fossil wood with well-marked growth rings. A rich and varied fauna, including ostracods, branchiopods, fresh-water gastropods and lamellibranchs, insects, fish and reptiles, also makes its first appearance here.

The Upper Karroo sediments (Escarpment Grit to Forest Sandstone) are characterised by *Dicroidium* and *Rhexoxylon* floras as well as by reptilian faunas. *Glossopteris* has not been found. No fossils are known from the sediments included in the basalt lava flows.

The Dwyka deposits clearly indicate that the Karroo System in the Federation began under glacial conditions. After this, the flora of the Lower Wankie Sandstone is too little known to be used as a climatic indicator, but the 40 ft thick Wankie coal seam and succeeding rich Upper Wankie Sandstone flora indicate good conditions for plant growth. The curious admixture of the ' Northern element ' species with the *Glossopteris-Gangamopteris* flora suggests a warming of the climate, since the former are believed to have lived in a warm climate in Europe. For the same reason it is questionable whether *Gangamopteris* necessarily always indicates a very cold climate, a view also held by Jongmans and by Teixeira (*C.R.3ieme Congr. Strat. Geol. Carb. Heerlen*, II, 627–630, 1952).

Climatic improvement, with increasing warmth, continued through Madumabisa Shale time. This is suggested particularly by (1) the fresh-water limestones, which may indicate the drying of lakes to form shallow pools, (2) the concretionary limestones, probably formed in wind-blown dust, and (3) the incoming of Crustacea (Leaiadidae), typically found in the Upper Carboniferous Coal Measures of the Northern hemisphere.

The Upper Karroo (Triassic)h flora s include *Rhxylon* and the conifer-like *Dadoxylon*. Large trunks of these genera, showing well-marked growth-rings, usually occur in the coarser, often conglomeratic deposits, suggesting seasonal variations of climate, probably associated with periodic heavy rainfall. At several stages no plants are yet known but their presence is indicated by herbivorous reptiles.

Finally, widespread fossil dunes of wind-blown sand indicate a hot, dry desert.

The lithology and palaeontology of the whole Karroo sequence in Rhodesia and Nyasaland thus show a progressive change from glacial conditions by warming and desiccation of the climate, frequently interrupted by seasonal torrential rains.

THE FRESH WATER FAUNA OF GOUGH ISLAND (SOUTH ATLANTIC)

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Introduction

Although the majority of the world's oceanic islands have now been visited by expeditions, and the chief components of their fauna are known, very little ecological information is available about them. Most expedition reports are fauna lists, interpreted along biogeographical and systematic lines and until recently the way of life of the species has received scant attention. It is for this reason that the present paper has been prepared. Admittedly incomplete, it may help to fill a large gap and stimulate research in a potentially rewarding field. It describes observations made on the fresh water fauna of Gough Island

(South Atlantic Ocean) during a six months residence between November, 1955 and May, 1956, while the author was a member of the Gough Island Scientific Survey. General accounts of this expedition have been given by Heaney & Holdgate (1957) and Holdgate (1958).

Despite brief visits by several passing expeditions, this remote island had received little scientific study before. The only fresh water invertebrate known to occur was ‘ a water beetle ’ collected by the Scottish National Antarctic Expedition in 1904 (Rudmose Brown, 1905) ; no identification of this specimen has ever been published and a recent search failed to discover it among the expedition’s collections (Brinck, 1948).

Gough Island

Gough is a volcanic island, probably initially of Tertiary age (LeMaitre, 1959). A thin ash band in the lower peats of an upland bog suggests that the last slight activity occurred about 2350 years ago (Hafsten, 1960). It rises on the Mid-Atlantic Ridge in latitude 40° 20′ S., longitude 9° 54′ W., and lies approximately 1500 miles from South Africa and over 1750 miles from the nearest point of South America. The three islands of Tristan da Cunha, Nightingale and Inaccessible (here spoken of as ‘ the Tristan group ’), lie 230 miles north-north-west and are the nearest land. Gough Island is roughly oblong in outline (Fig. 1), measuring about 8 miles (13 km.) by 4 (6½ km.), and its terrain is very rugged. The highest summit reaches 2986 ft (910 m.) and about half the total area lies above the 1500 ft (450 m.) contour (Heaney & Holdgate, 1957). Despite its classification

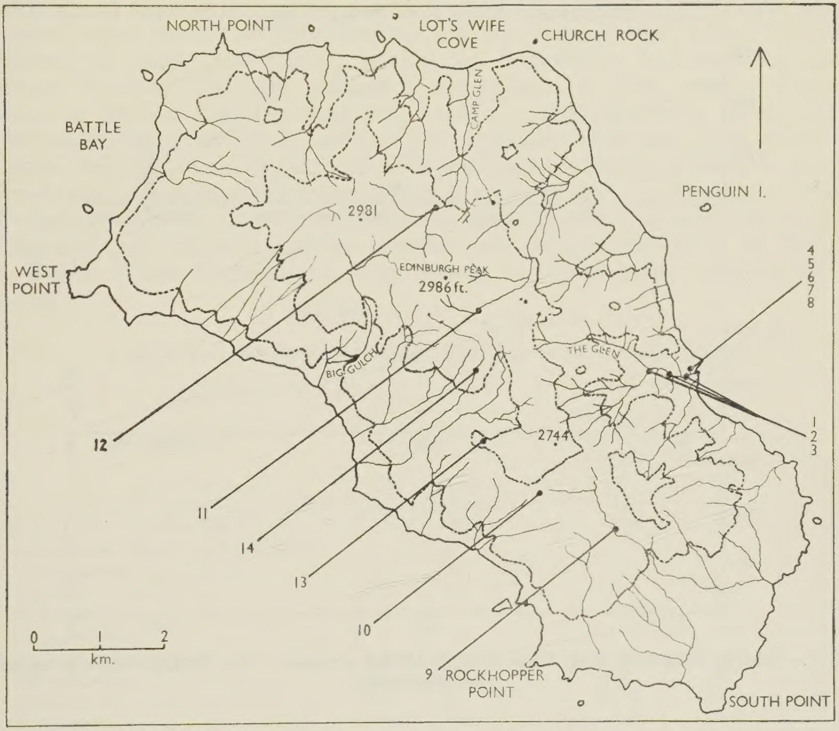

Fig. 1.—Gough Island. The broken lines represent the 1000 ft and 2000 ft contours : spot heights are also in feet. The positions of collecting stations 1–14 are shown.

as ‘ sub-antarctic ’, and its position just south of the sub-tropical convergence, the island has a temperate oceanic climate. During the years December, 1955–December, 1957, the mean temperature recorded at sea level on the east coast was 11·7° C., the extreme maximum in this period being 23° C. and the extreme minimum 0·4° C. Frosts are unknown at sea level, but ground frost and brief snow lie were observed above 2000 ft (600 m.) as early as March, 1956, and certainly occur more or less frequently on the uplands in winter. The mean annual rainfall at the Weather Station during the years mentioned above was 3225 mm. (129 in.), and observations made over a 3-month period in the summer of 1955–56 suggest that about 1·3 times as much rain falls on the uplands at 600 m., in the north of the island. There is a slight winter rainfall maximum.

Fresh Water Habitats on Gough Island

The uppermost levels of Gough Island have a rather subdued relief, and extensive plateaux occur at about 2100 ft (640 m.) and 2350 ft (715 m.). A few small pools on these uplands provide the only static fresh water habitats on the island. The upland streams are fairly slow-flowing and drain wide tracts of bog, but they nearly all spill over waterfalls into the heads of valleys now cutting back into the plateaux (Fig. 2). Their middle reaches are highly torrential, with frequent cascades, and many valleys are truncated seawards by cliffs between 100 and 500 ft, (30 and 150 m.) high, over which the water falls. Gently flowing lowland streams are absent, and even the main stream in The Glen, which has cut its channel down to sea level, has a mean gradient of a little under 1 in 10 over the last half-mile of its course.

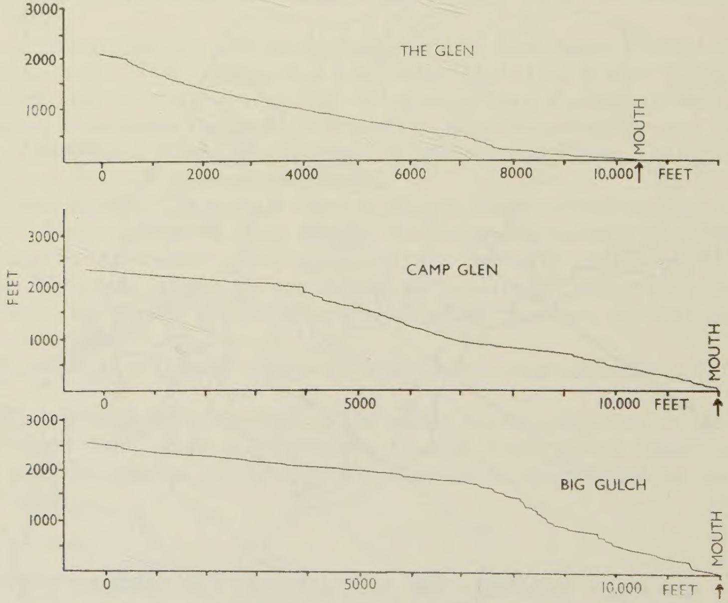

Fig. 2.—Profile diagrams from three Gough Island streams. The vertical scale is equal to the horizontal.

As would be expected from the terrain, the run-off of water is rapid and stream levels fluctuate widely and suddenly. These oscillations must be partly damped down by the action of the upland peat bogs as reservoirs, but a few hours heavy rain can cause The Glen stream to rise from a foot-deep brook to a bank high torrent three feet deep and almost impossible to ford. The main effect of the water retention by upland bogs is the provision of a steady flow during dry spells (which rarely last more than 2 or 3 days). Smaller side-streams lacking upland catchment may dry up completely after a brief drought, and their fauna in consequence becomes restricted to pools.

In such a severe habitat the general absence of aquatic vegetation would be expected, even without taking the geographical isolation of the island into account. Patches of bryophyte mat occur on some banks and boulders, and there is a characteristic bankside association of higher plants, among which Cyperaceae are prominent (Wace, 1960). Some of this vegetation is liable to intermittent flooding, and in smaller runnels it may overhang or dip into pools. But in general, neither an emergent nor a submerged macroscopic vegetation occurs in any of the island's watercourses. A felt of filamentous green algae and diatoms does however cover much of the surface of submerged stones.

Following the recent work of Gorham (1957) (1958) and Gorham & Cragg (1959), one would expect high sodium chloride concentrations in the natural waters of so oceanic an island. Table I shows the results of analyses of two samples taken from The Glen stream, and one from a small lateral tributary draining the slope immediately behind the Expedition Hut (now the South African Weather Station). Sample 1 comes from a point close to the pool chosen as Station 1 in The Glen (cp. Table 2) ; sample 2 from about 100 m. downstream from Station 2, and sample 3 from the lowermost pool, which was Station 1 on the subsidiary stream. The analyses are therefore likely to provide a good representation of the composition of water in the actual habitats studied. All analyses were carried out in the Division of Chemical Services (Department of Agriculture), Pretoria, and the samples were collected by Mr F. M. McAll of the Public Works Department, Cape Town, to whom I am indebted for the figures.

TABLE I.—Analyses of water samples from Gough Island

Components	Samples					
	(1)	(2)	(3)	Ireland (4)	Falklands (5)	World (6)
pH at 20° C.	5·7	5·9	5·0	4·4	4·1	...
Components, (parts per million) :						
Total solids	50	45	103	...	...	...
Sodium	16	14	...	12·5	38·6	8·4
Calcium	2	4	...	0·8	2·1	29·8
Magnesium	1	...	...	1·8	5·4	5·0
Sodium bicarbonate	8	...	...	...	...	...
Bicarbonate	18	12	...	*nil*	*nil*	52·0
Chloride	21	21	...	20·6	72·0	8·3
Sulphate	*nil*	*nil*	...	7·7	13·4	17·7
Nitrate	*nil*	*nil*	99	*nil*	*nil*	1·3
Ammonia, saline and albuminoid	0·13	0·08	0·88	...	...	...
Temp. hardness as $CaCO_3$	10	10	...	...	...	...
Oxygen absorbed in 4 hrs at 27° C.	6·8	7·3	10+	...	...	...

(1) and (2) from the Glen stream, (3) from a subsidiary stream (the sample too small for complete analysis). (4) Bog pool in Connemara (Gorham, 1957). (5) Bog waters in the Falklands (Gorham & Cragg, 1959). (6) World average fresh waters (Conway, 1942).

Comparing these figures with those of Gorham & Cragg (1959), Gorham (1957) and Conway (1942), it is clear that these stream samples approximate more nearly to the western Irish bog pools than to the Falkland Island waters.

Differences in the methods of collection and analysis make too close a comparison unwise. But it is evident that the Gough Island samples resemble the Irish ones in the levels of sodium and chloride, and the preponderance of these ions ; at the same time the waters are far less saline than those of the Falklands, which lie further into the west wind belt and have a much lower rainfall and less rapid run-off of water. The high nitrate figure for sample 3, the ammonia figures for samples 1, 2 and 3, and the relatively high rates of oxygen absorption, all indicate a high content of organic matter in the Gough Island waters. This was in fact largely peat ; the streams were yellowish in colour even in dry spells and became a dark brown in floods. But the penguin rookery in The Glen, which drained into the main stream above the site of sample 1, and the abundant ground-nesting birds all over the lower slopes, may also have added to the organic content.

THE AREAS SAMPLED

On Fig. 1, a sketch map of Gough Island, the main collecting stations for freshwater invertebrates are indicated. These fall into three groups (the numbers refer to Fig. 1 and Table II) :

(a) Main lowland stream stations. All of these lie on The Glen Stream. The first (1) lay near the Expedition Hut, only 30 m. from the sea and 5 m. above it ; the stream at this point lacked deep pools and ran swiftly over a stony bed. The second station (2) was 250 m. from the sea and 45 m. up, and this was a wider pool with some accumulation of fine gravel in a backwater. The third station (3) was at the main bifurcation of the stream, 600 m., from the sea and 75 m. above it. Here, a pool about 1 m. deep with a bed of medium-sized stones was sampled.

(b) Subsidiary lowland stream samples. A small runnel draining the flanks of the Glen immediately behind the hut was chosen as typical of minor tributaries of The Glen stream. Its course consisted of pools up to 1 m. deep, separated by waterfalls and rapids (Fig. 3). During the 225 m. of its course it fell about 150 m. Unlike the main stream it often dried to a trickle during brief periods of drought. The four major pools in the lower part of its course were sampled (4, 5, 6, 7), and the waterfall faces (8) and rapid reaches were also examined.

(c) Upland pools and streams. Streams were sampled briefly at 450 m., in Gonydale (9) and at 630 m. on Tarn Moss (11) while more careful examinations were made at 630 m. above High Camp (12) and 660 m. on Baseline Ridge (14). All of these were permanent watercourses with stony beds, though they were of course narrower than The Glen stream and never carried the same volume of water. Pools were investigated on Low Hump (645 m.) (13) and on the col between West Rowett and Green Hill (540 m. : 10).

The fauna revealed by this sampling was in all areas extremely scanty (Table II). The chief species will be discussed individually ; here it is only necessary to note the following general features.

1. Station 2 in The Glen stream, with 6 aquatic species present, is the richest station. This feature almost certainly reflects its comparative shelter with accumulations of fine gravel among the larger stones.
2. Only two species were ever encountered in the mountain streams, and often only one was present, while only one lowland station had fewer than three species. There is thus a correlation between species distribution and altitude.
3. The area of wet moss on a waterfall face in the minor stream, sampled as station 8, yielded only semi-aquatic and terrestrial species.
4. Terrestrial animals (*Porcellio scaber* and *Cylindroiulus latestriatus*) were seen in several stations. The latter was commonly washed down the

stream ; the individuals of the former which were collected were walking about in partly submerged vegetation. Undoubtedly other terrestrial animals (Gasteropoda, Collembola, enchytraeids, mites) are occasionally carried into the streams since landslips are frequent on the steep valley flanks and peaty material is invariably washed down after heavy rain (Wace, 1961). An added source of food for the carnivorous aquatic fauna is provided by carcasses of the ground-nesting Procellariiformes which are extremely numerous on Gough Island. Dead birds were seen in The Glen stream on several occasions, and pairs of wings conjoined by the pectoral girdle, the remains of victims of the Southern Skua (*Catharacta skua*) were common.

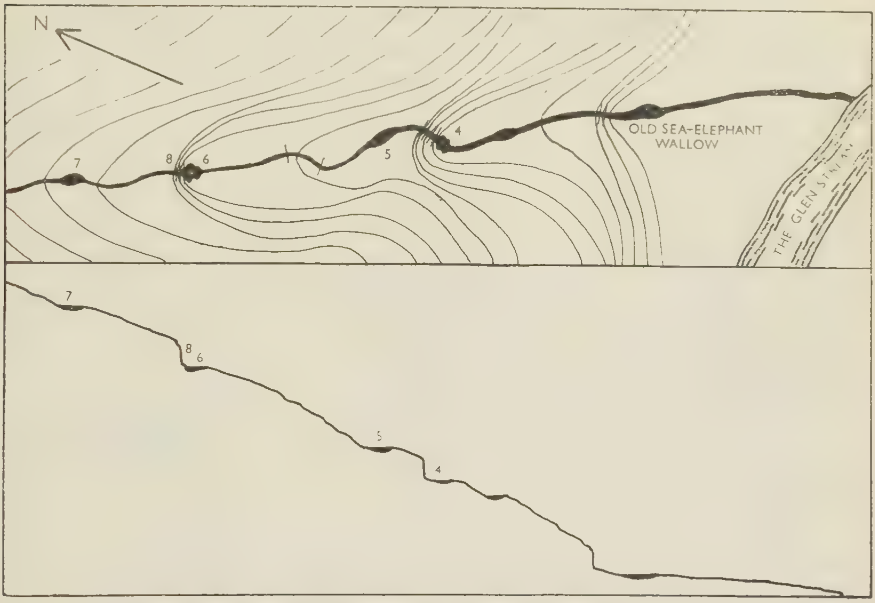

Fig. 3.—Sketch map and profile diagram for the minor lowland stream, showing the position of stations 4–8. Form-lines sketched : approximate overall distance from pool 7 to stream mouth, 200 yards.

5. The poverty of the fauna recorded in Table II might suggest incomplete collecting. But the collecting was supplemented by casual observation over a long period (the main pathway to the uplands follows The Glen stream). Furthermore, the drinking water supply for the Expedition was piped from the lowermost pool (station 4) on the minor stream and owing to the lack of filter, many aquatic animals were captured from it. Only the two Dytiscids and the Ephydrid larva recorded in the table as occurring in this stream were taken during a ‘ sampling period ’ lasting four months.

Furthermore, of the fresh water habitats observed on Gough Island, only one was not sampled—brackish pools and sea-elephant wallows which occur in a few places just above high water mark. It is very likely that larvae of certain Nematocerous flies (*Telmatogeton sancti-pauli* : a *Psychoda* species, a Chironomid sp. and a *Bradysia* (Sciaridae) sp.) inhabit moist supra-littoral situations, and some of them may perhaps be aquatic or semi-aquatic in such pools. Beyond these, it is unlikely that this omission has reduced the list appreciably. It is therefore considered that the poverty of fauna revealed in Table II is a genuine feature of the island.

THE ECOLOGY OF THE PRINCIPAL SPECIES

(1) *Dimecoenia tristanensis* Frey. (Diptera : Ephydridae).

Larvae of this fly are the most abundant and most highly adapted fresh water animals on the island. They are common in the larger permanent streams below 450 m., and occur sporadically above this height (Table 2). They were notably

TABLE II.—The distribution of aquatic and semi-aquatic animals on Gough Island

Locality	The Glen			Minor Stream					Uplands					
Altitude (m.)	5	45	75	15	17	20	25	24	450	540	630	630	645	660
Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14
SPECIES :														
1. *Dimecoenia tristanensis* Frey (Dipt : Ephydridae)														
larvae	+	+	+	+	–	–	+	–	+	–	+	–	–	–
pupae..............	–	–	–	–	+	–	–	–	–	–	–	–	–	–
adults (in or near water)	+	+	+	+	+	+	+	+	+	–	+	–	–	–
2. *Lancetes varius* (F) ssp. *dacunhae* Brinck (Coleoptera: Dytiscidae)														
adults	+	+	+	+	+	+	+	–	–	+	+	+	+	+
larvae	–	+	–	+	+	+	+	–	+	–	–	–	–	+
3. *Bidessonotus involucer* Brinck. (Col : Dytiscidae)														
adults	–	–	–	+	+	+	+	–	–	–	–	–	–	–
4. Dipteran larva, indet.	–	+	–	–	–	–	–	–	–	–	–	–	–	–
5. Tipulid larva, indet. ..	–	–	–	–	–	–	–	+	–	–	–	–	–	–
6. Noctuid larva, pupa ..	–	–	–	–	–	–	–	+	–	–	–	–	–	–
7. ? *Quedius* sp. (Col : Staphylinidae)														
larva	–	–	–	–	–	–	–	+	–	–	–	–	–	–
8. Acarine sp. indet.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
9. *Iais pubescens* (Dana) (Isopoda : Jaeridae)	–	+	–	–	–	–	–	–	–	–	–	–	–	–
10. Enchytraeidae sp. ? ..	–	+	–	–	–	–	–	–	–	–	–	–	–	–
11. Enchytraeidae sp.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
12. *Procerodes ohlini* (Bergendal) (Turbellaria : Procerodidae)	+	+	+	–	–	–	–	–	–	–	–	–	–	–
13. ? Porifera sp. (Indet. fresh water sponge)	+	–	–	–	–	–	–	–	–	–	–	–	–	–
TERRESTRIAL SPECIES :														
14. *Porcellio scaber* (Isopoda)..........	–	+	–	–	–	–	–	–	–	–	–	–	–	–
15. *Cylindroiulus latestriatus* (Diplopoda)	+	+	–	+	–	–	+	–	–	–	–	–	–	–
TOTAL AQUATIC SPECIES IN WATER	4	6	3	3	3	2	3	0	2	1	2	1	1	1

less numerous in the minor stream sampled in The Glen, due perhaps to the intermittent nature of the flow and the great variation in its rate.

Eggs are laid on stones exposed to a moderate current, the ovipositing adults walking under water. While submerged they retain an air film over the body and between the wings. In this behaviour the species closely resembles members of the nearly related genus *Ephydra,* including *E. hians* (Say) (Williams, 1938).

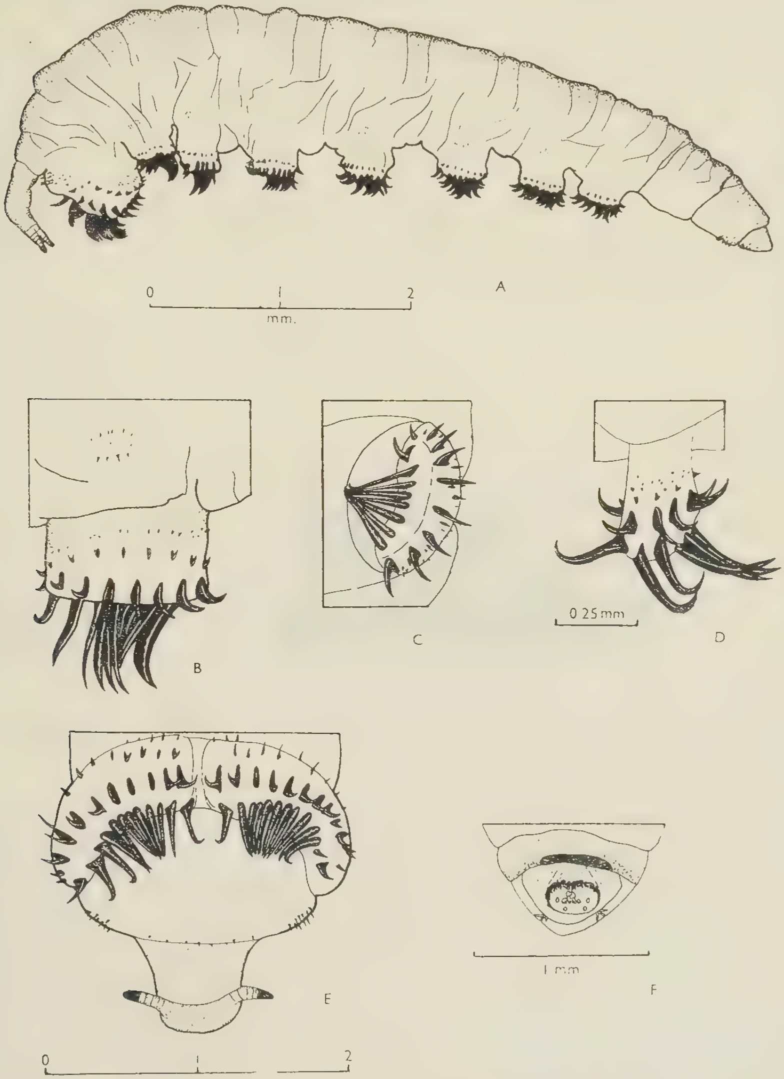

FIG. 4.—Larvae of *Dimecoenia tristanensis* Frey (Diptera: Ephydridae). A = camera lucida drawing of whole animal (somewhat distorted by spirit preservation). B = abdominal limb, contracted position, from side. C = the same, from below. D = abdominal limb in supposed expanded position. E = terminal posterior region, with spiracular processes. F = mouth region, showing supposed rasping spine-tracts.

The larvae cling to stones in a moderate current, using rosettes of stout hooked spines which are borne on seven pairs of small stumpy prolegs and an eighth broader posterior pair (Fig. 4). In preserved specimens these hooks are usually held in a retracted position, but they can probably be spread far more widely in life, and Fig. 4 d gives some indication of the likely arrangement when in use for grappling to the substratum. The larvae are not permanently attached in one position ; they are easily dislodged by a probe and probably distribute themselves actively in accordance with available food. Judging from the way in which they accumulated on clothes left to rinse in pools in The Glen stream this active distribution involves not only slow walking over the stones but occasional drift (perhaps involuntarily) downstream in the current.

The oral region does not bear any elaborate ' filter feeding ' apparatus. The mouth is guarded by two patches of small spines which may serve as rasping jaws (Fig. 4 f). Examination of the gut contents of two selected examples showed the food in each case to consist of diatoms and algal filaments, probably identical with those composing the surface mat on the stones in The Glen stream, thus suggesting that they feed by browsing upon the surface felt.

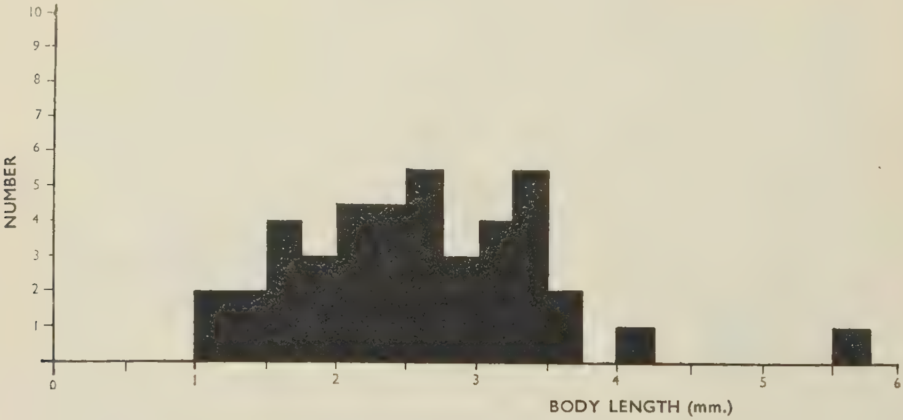

FIG. 5.—Block histogram showing size distribution in a sample of 42 larvae collected from the same station on 5.12.55.

Rough measurements of overall length (along a standard line on the body) of a sample of 42 preserved larvae, collected in The Glen stream on 5.12.55 are plotted in Fig. 5. They suggest either a variable growth rate or a wide age-distribution within the population. The latter is considered more likely. Larvae remained abundant in the stream from December through until late March, perhaps falling off in numbers in April. Adults were extremely common along the banksides throughout these summer months (becoming at times a positive nuisance to heated travellers). It seems certain that the species has no rigid annual breeding cycle ; probably a number of summer generations occur, being determined directly by climate.

Only a few pupae of this species have been collected (Fig. 6). There is a suggestion that they occur in bankside situations less exposed to the current than do the larvae, and the smaller hook-rosettes which they bear might support this. Like the larvae, they are attached to stones by these hooks.

Adults range some distance from the watersides, and were encountered frequently in sweepings of rank fern and mixed vegetation on the sides of The Glen, though nowhere very high on the slopes. They were also abundant in rank vegetation at the top of the beach between The Glen and Dell Rocks, and were taken at light traps at the Expedition Hut on several nights. Their distribution in streamside localities is indicated in Table 2.

Dimecoenia tristanensis is therefore a truly fresh-water animal on Gough Island, with highly adapted torrent-dwelling larvae ranging in the streams from a few metres to 660 m., above the sea. This behaviour seems to differ from that assigned to it by Frey (1954) on the basis of material collected by the Norwegian Scientific Expedition to Tristan da Cunha 1937–38 (Christophersen, 1946). Frey writes : ' Ein echter halophiler Endemit ist schliesslich *Dimecoenia tristanensis* Frey, deren larven in Brackwasser und Süsswassersammlungen in der Nähe des Meeres häufig vorkamen.' The actual locality records for the larvae and pupae (which are not listed separately by Frey) include :

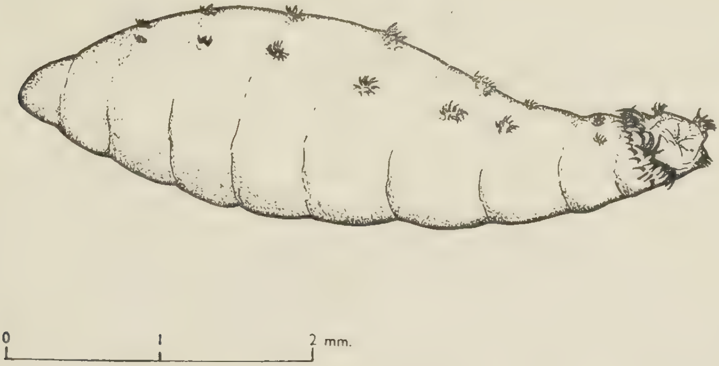

FIG. 6.—Pupa of *Dimecoenia tristanensis* Frey, from a camera lucida drawing.

FRESH WATER—

- ' brook with quite a strong current '
- ' probably from brook running near the Expedition buildings ' (at about 50 m.)

BRACKISH WATER—

- ' pond with brackish water, containing both fresh water and salt-water algae.'
- ' pool . . . stagnant and presumably brackish . . . with a mixture of sea-water and fresh-water algae.'
- ' sea-water pool on beach, cut off from sea but on so low a level that the sea-water now and then has access to it. Vegetation in the pool—*Enteromorpha*.'

BEACHES AND LAND—

- ' tussock and convolvulus land, rather dry, with a good deal of quicksand in between.'
- ' large grasslands on plateau about 30 m. above sea level, sloping gently towards the sea.'

The last two localities appear somewhat atypical although they may have included damp marshy patches which would be a normal haunt of Ephydrid larvae. By comparison with Gough Island, however, the startling fact emerges that the Norwegian Expedition, which certainly ascended the uplands of Tristan da Cunha and Inaccessible Island, nowhere collected *D. tristanensis* larvae further than 50 m. above sea level and found most of their specimens in distinctly maritime habitats. Furthermore, only two adults of this species were collected by them (Frey, 1954) ; a figure in striking contrast to the 63 individuals obtained by the present author (Oldroyd, 1958) in what were no more than representative gatherings spanning the same season. The collecting on the two islands was not truly comparative, but it is difficult to escape the suggestion that *D. tristanensis* differs in its abundance and ecology upon them.

If Frey is correct in describing the Tristan population of *D. tristanensis* as halophil, and if this was the habit of the ancestor from which this endemic species was derived, then the Gough Island representatives are clearly recent invaders of fresh-water torrents. The species has most probably been derived from a South American stock (the genus is not known outside America). Cresson (1931) describes two *Dimecoenia* species from Southern Chile, but gives no indication of their larval habitat.

(2) *Lancetes varius* (F) *ssp. dacunhae* Brinck. (Coleoptera : Dytiscidae).

This is the most widely distributed aquatic animal on the island, ranging from sea level to 2200 ft (670 m.) and often being the sole inhabitant of upland pools. Larvae were taken in streams over a similar altitudinal range. The adults are full-winged and capable of flight, and they show no difference from the Tristan da Cunha population of the same sub-species (Balfour Browne, private communication). On that island it similarly ranges from brackish-water pools at sea level to mountain lakes at 750 m. (Brinck, 1948). Brinck comments ' as expected from the structure of the imago and the larva, however, it lives chiefly in stagnant waters ; yet it has several times been encountered in slowly running water in widened brooklets.' On Gough Island, while certainly present in still waters, the species is quite common in swift torrents. In The Glen stream the adults show a characteristic cryptic habit when disturbed, diving into gaps between stones and actively working their way among or under small pebbles. It is probably this habit which permits the species to live in torrents which when in full flood, run so strongly that a man finds it difficult to stand in no more than 3 ft of water. Even so, some individuals are dislodged in floods, as witness their appearance in the piped Expedition water supply.

Like all Dytiscids the animal is carnivorous and in the main lowland streams it may feed on *Dimecoenia tristanensis* larvae. But in many places its range extends outside that of all other known freshwater invertebrates. In upland pools and probably even in lowland sites like the small runnel near the Expetion Hut, where the fly larvae are rare, terrestrial animals must contribute largely to the diet. In this habit the species resembles *Rantus pacificus*, a Dytiscid which inhabits streams up to the 3500 ft level on Hawaii, and has been shown by Williams (1936) to feed on terrestrial invertebrates. Even in continental areas aquatic beetles may derive a significant part of their food from these sources. Crisp (1961) has demonstrated that *Agabus* and *Gyrinus* species in northern English upland reservoirs take non-aquatic Diptera in quantity. The occurrence of millipedes, isopods, other invertebrates, and bird carcasses, in the streams of Gough Island has already been mentioned : such animals may form the normal diet of aquatic carnivores on oceanic islands.

(3) *Bidessonotus involucer* Brinck (Coleoptera : Dytiscidae)

This small beetle was encountered only in the smallest and most weed-fringed of the watercourses examined. Adults were alone taken, and were commonest among partly-submerged vegetation. This compares with the type locality for the species on Inaccessible Island ' among plants in a rivulet ' (Brinck, 1948). The most interesting feature of this species is its reduced wings and incapacity for flight : despite this Mr J. Balfour Browne and Professor Per Brinck, who have compared Gough and Inaccessible material, find only slight differences between them. The food of these beetles is unknown, but owing to their small size (1·6–1·7 mm. long), small terrestrial animals such as mites, Collembola and Enchytraeidae appear more suitable than any members of the known aquatic fauna.

(4) *Iais pubescens* (Dana) (Isopoda : Jaeridae).

A small number of isopods of this species were taken in The Glen stream (Station 2) 250 m. inland and 45 m. above sea level. The record is interesting because this is normally a marine species and it occurs between tide marks on The Glen beach, near the stream mouth, commensally upon the Sphaeromid *Isocladus tristensis.* Dr K. H. Barnard, who identified the material has drawn my attention to a comparable record of the species free-living in brackish water in the mouths of streams on the west coast of the South Island, New Zealand (Chilton, 1909). The record from Gough Island is however the first for it in a fully fresh-water habitat.

(5) *Procerodes ohlini* (Bergendal) (Turbellaria : Procerodidae)

Although widespread in The Glen stream, this planarian was not encountered elsewhere on the island, nor is it known on Tristan (Westblad, 1951). In The Glen it is frequent under stones and among debris, but it was only once taken feeding, when 2 specimens were collected on the carcass of a broad-billed Prion (*Pachyptila vittata*).

As with the preceding species, the chief interest in the occurrence of *Procerodes ohlini* in Gough Island streams lies in its normal marine littoral habitat (Prudhoe, private communication). It is recorded from beaches in Tierra del Fuego and Kerguelen ; in the former area, as Mr Prudhoe has pointed out to me, it was noted by the Hamburger Magalhaenischer Sammelreise (1892–3) at Ushuaia ' under stones at the mouth of a stream above high water level '. The species does not occur in the littoral zone on Gough Island, where the related *P. variabilis* is common.

(6) Other species

Three other aquatic invertebrates were collected in The Glen stream :

The fine gravel in the most sheltered part of Station 2 yielded 3 specimens of a thin, bright red, oligochaete. All these were immature and have proved unidentifiable (Roots, private communication).

From the same gravel a single white apodous dipteran larva was obtained.

At Station 1, nearer to the mouth of the stream, several specimens of what was supposed in the field to be a fresh-water sponge, were collected. Unfortunately these cannot now be found among the Expedition's material in the British Museum, and no identification is therefore possible.

General Ecology of the Aquatic Fauna

The preceding observations give some idea as to the habits of the principal Gough Island aquatic animals, and Fig. 7 summarizes the known altitudinal range of all the species recorded in the fresh waters of the Tristan da Cunha–Gough group. The first thing which is immediately apparent is the numerical preponderance of carnivorous species (3 Dytiscidae and a planarian) : the Ephydrid *Dimecoenia tristanensis* is the only common phytophagous animal. Furthermore, at least one of these carnivores, the Dytiscid *Lancetes varius* ssp. *dacunhae*, seems to range into habitats in which no other aquatic species are available as food. This is presumably possible only because terrestrial species are readily substituted.

There is no clear evidence at present that any one species within the island fresh water fauna is dependent on any other : at least this dependence is in-sufficient to limit distribution. On the other hand the ranges of these animals may perhaps be correlated with certain habitat factors. *Bidessonotus involucer* seems to succeed only in small runnels near the sea and partly obstructed by vegetation. *Dimecoenia tristanensis* appears to be most abundant in permanent streams with a steady flow: its absence from the uplands may reflect low temperature, or prevailing strong winds which are inimical to adult dispersal. *Procerodes ohlini* may be restricted by large waterfalls: there are no wading or dabbling birds which might assist its spread. *Lancetes varius*, a strongly flying, active insect alone seems able to reach and exploit most of the aquatic habitats available.

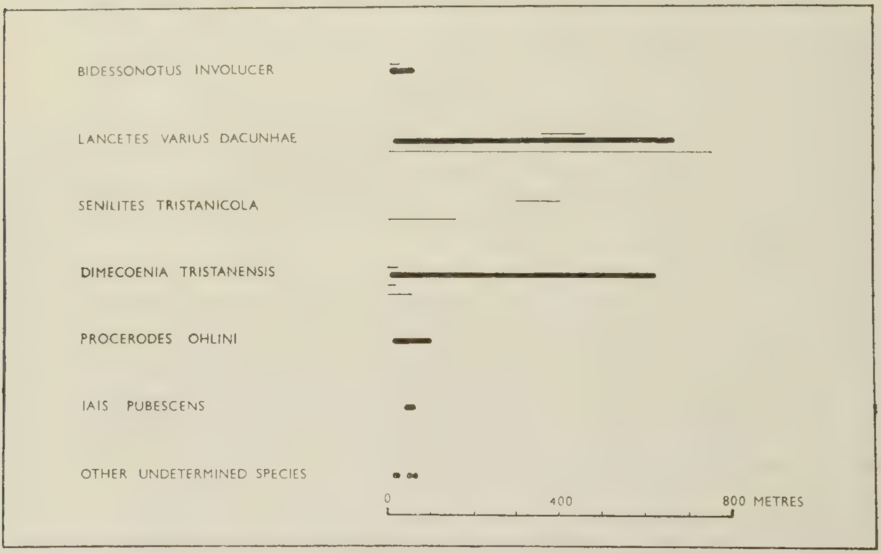

FIG. 7.—The altitudinal ranges of Tristan da Cunha and Gough Island aquatic animals. Heavy lines = Gough Island records. Light lines = records from the other islands.

The suggestion that these few colonists have been able to take up ranges limited directly by habitat factors, rather than by competition or predation must remain tentative. Such behaviour is however to be expected in the initial stages of occupation of an environment, while the latter is grossly under-exploited. But the assessment of the degree of under-exploitation is very difficult. By analogy with a continental area—even with a barren mountain torrent—the Gough Island streams are certainly species-poor. In number of individuals, however: in terms of production of animal matter, the difference may not be so great. Certainly *Dimecoenia tristanensis* larvae were strikingly abundant during January and February 1956.

The presence of two marine animals in the main stream of The Glen is probably a better indication that interspecific competition is slight. Such species must be assumed to be at a disadvantage when competing with established fresh water forms: in some groups (like fishes) there are well-known 'complementary' species which invade fresh water only when better-adapted species are absent (Myers, 1953). This interpretation is the most generally favoured one for the presence of from 10 per cent to 40 per cent of species of direct (and fairly recent) marine ancestry in the streams of remote islands. The invasion of such streams may also be favoured by their relatively high sodium chloride content (Table I).

This latter feature may help to offset the abruptness of the transition in conditions in the mouths of rapid island streams, where a true brackish-water zone is narrowed to tiny dimensions by the combination of steep gradients and small tidal range.

It would be easy to attribute the absence of many animal groups from these islands to distributional factors, and to see in the lack of molluscs, Plecoptera, Trichoptera, Ephemeroptera, Simuliidae and Blepharoceridae further evidence of the under-exploitation of habitat. There is no doubt that such an inference is partly valid. Many of these groups reach no oceanic island in the world, yet it is virtually certain that suitable environments are present in most places. Equally, there is no doubt that streams such as those on Gough Island would never support a rich fauna. The total absence of rooted or floating aquatic plants is probably due to the scour of the current rather than an inability of the native Cyperaceae and Gramineae to form some kind of swamp, as tussock grasses do on Nightingale Island (Hafsten, 1951 ; Hagen, 1952). Even the algal flora may be reduced by the severity of the habitat, as it is in the Azores (Bourrelly & Manguin, 1946). The absence of fresh-water mollusca may well be attributable to such botanical deficiencies as much as to dispersal problems. Even if a random assemblage of continental aquatic species did succeed in reaching Gough Island, under present conditions there is no likelihood that all of them would become established.

DISCUSSION

Two features of the Gough Island aquatic fauna will be considered here : its probable origin and history, and the extent to which it typifies the fresh-water fauna of oceanic islands in general.

There is little doubt that the Tristan da Cunha–Gough Island group arose by isolated mid-oceanic eruption, and has never been more closely connected to any continent. Holdgate (1960) has suggested that both the islands and their faunas are relatively young, and that the vast majority of the terrestrial invertebrates arrived as air-borne immigrants from South America. Certainly the faunal relationships with that continent are much stronger than with any other. On taxonomic grounds it seems possible that the fresh-water animals on the islands did not arrive there at the same time : they may in fact be subdivided roughly into three groups :

(a) *Fairly ancient, ' autochthonous ' species*

Brinck (1948) regards the endemic, flightless, Dytiscid *Senilites tristanicola* Brinck *from Tristan da Cunha* as resembling most nearly the primitive genus *Anisomeria* Brinck from Juan Fernandez and Chile. It stands apart from the other aquatic insects in the four islands by virtue of its far greater distinctness from outside stocks : clearly, if it has undergone evolution to the level of an endemic genus in the islands it must have been established there for a considerable time. However, as Gressitt (1958) emphasizes primitive forms do tend to survive on islands where competition is low while parent stocks are replaced in the continents in which they originated, and the same argument may apply here. Whatever that may be, there is good reason to isolate *Senilites tristanicola* in a class by itself among the island aquatic fauna.

(b) *Species of intermediate age*

The small Dytiscid *Bidessonotus involucer* Brinck was regarded by Brinck 1 48) as also belonging to the autochthonous fauna of the islands. None the less, while a good species, it belongs to a genus ranging from Juan Fernandez and Patagonia to Australia and Asia. The chief peculiarity of *B. involucer* is its flightlessness : the slight differences between the Gough and Inaccessible Island populations suggest that these may have arisen from two independent winged immigrations which have lost their flying capacity in parallel. Such a trend is well known among the beetles of remote islands and mountains (Darlington, 1943), even though it is rare in Dytiscids (Brinck, 1948).

Dimecoenia tristanensis Frey is another species endemic to the Tristan group, but belonging to a widespread American genus. The Tristan and Gough populations have not diverged, perhaps because they have not been separated for long. The chief doubt about this species is its antiquity as a fresh-water animal. Despite its perfect larval adaptation for life in torrential streams Frey (1954) considered it a supra-littoral halophil, and it may anciently have had this habit. Invasion of fresh water by such animals is not unknown on remote islands : on Hawaii it has occurred in 5 species of the otherwise littoral Chironomid genus *Telmatogeton* (Zimmermann, 1948).

(c) *Relatively recent colonists*

The third Dytiscid, *Lancetes varius* ssp. *dacunhae* is believed by Brinck (1948) to be a very recent colonist of the islands, perhaps imported by whalers. Since it has attained sub-specific distinctness, and since it belongs to a genus widespread in America and represented by endemic species in Juan Fernandez (Zimmermann, 1924), the Falklands (Champion, 1918) and South Georgia (Enderlein, 1911), there seems however no real reason to doubt that it has reached the Tristan group by natural means. In any event, its close resemblance to the South American parent species is good evidence of its recent arrival.

Similarly, the two marine species, *Procerodes ohlini* and *Iais pubescens* must be regarded as recent invaders of the Glen stream. It is rare to have a single species occupying both a marine and freshwater habitat (Prosser, 1955 ; Lockwood & Croghan, 1957) ; normally there is a clear taxonomic divergence of the two stocks. Since this divergence has not taken place on Gough Island it is reasonable to assume either that these species have not long occupied their present range, or that they are tolerant ' complementary ' animals capable of interchanging and interbreeding with members of a littoral population. This second explanation seems unlikely, for the planarian at least (especially as it is not recorded in the littoral), even if it is more plausible for the isopod.

Although nothing is known about the rates of evolution of endemic species, it seems likely that the fresh water animals on Gough Island have colonized the island over a wide period. The random nature of this process, which is presumably followed by a spread to the limit of the accessible habitat, makes their unrelated distribution patterns on the island rather easier to understand.

An evaluation of the extent to which the Gough Island fauna is typical of oceanic islands as a whole would require a far more lengthy review than is practicable here. In many of its features it does however appear typical. Extreme impoverishment has long been known to be a characteristic of insular fresh water faunas : furthermore those groups dispersed largely as air-borne adults may be arranged in order according to their relative success in reaching remote archipelagos. Plecoptera and Megaloptera are notoriously unsuccessful : Trichoptera and Ephemeroptera only slightly better : Hemiptera and Odonata rather more widespread : Diptera and Coleoptera, the two Orders represented on Gough Island, the most widespread of all. These two last groups alone have aquatic members on the southern cold-temperate oceanic islands like Kerguelen and the Crozets. The pattern is a consistent one also at the family level, the

Simuliidae, Culicidae, Chironomidae and Ephydridae being the most widespread Dipteran families with aquatic larvae.

Gough Island is also typical in having this scanty aerially-dispersed aquatic fauna augmented by direct colonization from the sea. All the fresh water fishes and Crustacea, and many of the aquatic molluscs of oceanic islands have originated, probably fairly recently, from marine stocks, and together they may make up 40 per cent of the total fresh water fauna. Relaxed competition is generally taken to be the factor permitting this ready invasion.

The third general feature of the Gough Island aquatic fauna which is probably of universal application among oceanic islands is the apparent diversity in the period of establishment of its members. This is to be expected on isolated volcanoes deriving their animal population by trans-oceanic immigration, and the present distribution patterns suggest that this process of expansion and colonization is still going on.

Summary

1. Gough Island (40° 20′ S. ; 9° 54′ W.) is one of the world's most isolated islands. It lies almost midway between South Africa and South America, and is of volcanic origin. Tristan da Cunha, 230 miles north-north-west is the nearest other land.

2. Torrential streams are the principal fresh water habitats.

3. Fourteen sample stations examined during the southern summer of 1955–56 yielded only 8 species of aquatic animal. Five are discussed individually. Three have also been recorded from fresh water on Tristan da Cunha : 2 are marine species not previously recorded from fully fresh water.

4. Carnivorous species appear to outnumber the others, and also to range most widely. Various non-aquatic food sources seem to be available for them. The most abundant individual species is however the Ephydrid dipteran *Dimecoenia tristanensis*, whose larvae feed on diatoms and algal filaments. There is no clear evidence that any aquatic species is especially dependent on any other : distribution appears to be related directly to habitat factors.

5. The aquatic fauna of the island seems to have been recruited from immigrants arriving at very different times.

6. The fauna appears typical of such habitats on remote islands.

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SYMPOSIUM ON QUATERNARY ECOLOGY

HELD IN THE ROOMS OF THE SOCIETY

ON DECEMBER 17TH AND 18TH 1959

Under the Chairmanship of: Professor C. F. A. PANTIN, F.R.S., Pres. L.S.; Mr A. W. EXELL, V.-Pres. L.S.; Professor L. J. AUDUS, V.-Pres. L.S., and Professor H. GODWIN, F.R.S.

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I. INTRODUCTION

By H. GODWIN, F.R.S.

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THE task of the Symposium, which it has been the happy inspiration of the Linnean Society to call, may be briefly stated: it is to consider what is known of the plant and animal ecology of different parts of the Quaternary Period in Britain. It will be concerned with Interglacial and Interstadial periods, with the highly recognizable Late-glacial Period that is now seen to lie within reach of radiocarbon dating, and with the Post-glacial Period up to historic times. This limitation follows directly from the fact that our evidence will be derived almost entirely from plant and animal remains within organic deposits such as lake-muds and peats, and that formation of such deposits is almost entirely limited to the temperate or mild periods that intervene and separate the cold severe glacial episodes themselves. One of the outstanding features of Quaternary Research of the last two or three decades has been the increasingly apparent wealth of biological and climatic evidence produced from the organic interglacial deposits, in contrast with the meagre and hardly-won yield from the far more extensive deposits of boulder clay, outwash gravel, loess and other glacial material of a mineral nature.

Each contributor will aim to show, within the field of evidence familiar to himself, how far it is possible to reconstruct the fauna and flora of given periods of the past, how far communities can be recognized, how they correspond with communities of today, how far the results show the operation of climatic, edaphic and biotic controls, and what conclusions of biogeographic importance may be drawn. We may in certain instances look forward to hearing of instances where both animal and plant communities have been investigated in one and the same deposit, so that we may judge what coincidence or conflict of results thus ensues.

Our contributors necessarily must concern themselves with the interplay between the geological and biological sciences. All our results rest upon the identification of fossil or sub-fossil material, the condition and recognizability of which are of the greatest importance to our conclusions. However, as compared with the more ancient geological periods, our later periods have the advantage that they involve, to a very large extent, species that are still living, and with whose ecological requirements we are more or less familiar.

To the kind of geology involved in these studies the ecologist can himself make considerable contribution, for in the study of a single organic deposit the geologist is faced with significant changes within inches, not hundreds of feet, with time scales where decades and not millenia are important. Few geologists have concerned themselves with such slight deposits and such minor and transient effects, but they are very often the outcome of processes perfectly familiar to the field ecologist. It is he who can recognize the stages of hydroseral succession of pond or lake, who recognizes the microtopography of an infilling salt marsh and the mechanisms at work there, and he who must follow the detailed manner of bog-growth or sand-dune accretion and decay. Particularly in his concern with organic materials he has been responsible for a system of lithology dependent upon recognition of the constituent plant and animal remains, and stratigraphic studies based thereon lead back at once to the successional changes in the communities now fossilized.

Per contra the Quaternary ecologist must always be dependent upon the maximum geological evidence that can be derived from the deposits whence he gets his material. He seeks from the total geological picture all the information possible upon the environmental conditions in which his sub-fossil plants and animals existed, and he may only interpret his own evidence as it appears against a precise picture of the geological stratigraphy and in the light of known geological correlations and climatic inferences.

All kinds of organic material contribute to establish these conceptions of former plant and animal communities, but there is no doubt that the exploitation of pollen analysis (palynology) has been the mainspring of the development of Quaternary vegetational history over the last quarter century or so. The amazing abundance and ubiquity of pollen grains and other spores gives them tremendous advantages : a frequency of hundreds or thousands to the cubic millimetre of deposit is something unmatched by other types of fossil. None the less it would be folly indeed to neglect to consider other kinds of plant fossil, and we shall therefore hear accounts of the identifications of fruits, seeds, leaves and wood, and of the macroscopic remains of beetles, mollusca and other animals. In all these instances it is frequently possible to recognize the organisms at the species level, a conclusion far less often attainable by pollen analysis, powerful as that method may be.

Furthermore, we ought, as ecologists, to concern ourselves not exclusively with either plants or animals, but to consider *in toto* all the evidence from a given deposit in the attempt to reconstruct the whole biocoenose represented. The late Mr S. Hazzledine Warren steadily pursued this aim in his remarkable studies of the Lea Valley Arctic Bed, a deposit now shown by radiocarbon assay to have an age of about 28,000 years. He brought together the evidence of a mammalian fauna containing mammoth, reindeer, lemming and others, of a depauperate and strongly boreal assemblage of mollusca, of a northern assemblage of mosses and of flowering plants, in which latter group arctic willows and subarctic and arctic-alpine plants of many categories were represented. Even closer to the scene of our present meeting is the site of the interglacial deposits recently found in Trafalgar Square, where once more remains of a wide range of plant and animal types have rightly and rewardingly been brought into consideration together.

Having said this much in general terms I may usefully return to the special bearing of pollen-analysis upon Quaternary Ecology. It can claim to be the basic study for this time not only because it is applicable to so many deposits, but because it operates to reveal the former existence of the great plant formations, which were extensive and stable communities altering only with climatic change. They were inevitably the sources both of food and of shelter for all other organisms, not excluding prehistoric man, and it is essential that they should be characterized and identified whatever further Quaternary study may be contemplated.

The original methods of L. von Post were based upon the recognition of former European climatic vegetational belts, and his research and that of his successors have indeed shown how the major forest zones altered and migrated under the compulsion of climatic changes during the Post-glacial period. As is well known, the consistency of these movements allowed the use of pollen analysis to supply a series of chronological zones against which geological, archaeological and other Quaternary events could be viewed.

Very greatly improved standards of identification, particularly by the use of oil-immersion microscopy, have now permitted the recognition of a large number of herbaceous plants, often at the species level, from Quaternary deposits of many ages. Thus the opportunity has been created of identifying the open plant communities characteristic on the one hand of the Full-glacial and Late-glacial Periods, and on the other, of the clearings made by prehistoric and recent agriculturalists as they have progressively destroyed the natural forest cover. We may expect to hear of many plant communities of this kind.

The interpretation of pollen analyses still calls for the greatest caution and skill, and many dangers beset the impetuous investigator. Dr J. Iversen, pupil of von Post, and one of the great leaders of the subject, holds the view (with which I concur) that all palynological interpretation must be based upon ecological experience : the lack of such experience can be responsible for extremely naive and unrealistic conclusions.

A primary difficulty is that a lake or bog surface that is incorporating pollen as its deposits accumulate, receives its pollen supply from a great area. The spectrum at one level will include that of the purely local vegetation of the bog surface, of the bog or lake-margin zones and of the whole countryside beyond. When, however, the pollen is abundant, the stratigraphy clear and macroscopic remains have been extensively identified, an experienced ecologist can often unravel the evidence and recognize the several separate components of the pollen spectrum. Thus we had recently undertaken, in our Sub-department of Quaternary Research in Cambridge, pollen analysis of glacial melt-water silts from a lake site in northern Scotland, and Miss R. Andrew had recovered a very extensive pollen flora from them. As to what vegetation might have given rise to such an assemblage, I sought the opinion of Professor Einar du Rietz of the Växtbiologiska Institution, Uppsala, a leading authority on montane and sub-arctic vegetation. Without citing the results which are indeed still incomplete, it is of interest to quote from his reply :

> ' Your fossil assemblage of plant species resembles very much our low alpine vegetation, exposed to the pollen rain from the subalpine birch forest and from the uppermost pre-alpine pine forest, e.g., on one of the lower alpine slopes on any of the mountains sloping into the Åbisko valley of Swedish Lappland. *Dryas* indicates definitely a calcareous facies of the low alpine heath, as does *Thalictrum* (*alpinum*?) and *Saussurea*, but the " very much

> *Empetrum*" and "abundant leaves of *Salix herbacea*" suggests that much of the vegetation must have belonged to the non-calcareous heath. The mixture of pine and birch pollen with heath and meadow species common to the low alpine and subalpine belts also suggests the possibility of open heath areas, due to solifluxion and strong winds in the subalpine belt, alternating with birch forest and some pine groves.'

Professor du Rietz later added that the presence of *Koenigia islandica*, along with other species, pointed to deposits of wet silt, perhaps in seasonally active melt-water runnels. His wide experience has clearly given an illuminating resolution of the pollen evidence.

There are many reasons why the local vegetational development of a site must be understood. Primarily knowledge of it is needed to separate the local influences in the pollen diagram from the regional, and secondarily to show how climatic and geological changes have registered themselves. Thus we can give precision to the analysis of a former marine transgression by identifying the salt marsh and its gradual replacement of fresh water fen : we may equally recognize a climatic overturn by seeing a layer of tree-stubs grown upon a bog surface in a dry period, overlaid and preserved by aquatic peat laid down in the subsequent wet period. The working out of the local development of a site is enormously facilitated by the examination of the sequence of mud and peat types and by identifying their content of twigs, leaves, fruit, seeds, algal and animal remains. With such information at hand the pollen diagrams become at once more meaningful and one can readily see how many of the component pollen curves move in the closest relation to the stratigraphic change.

The development of radiocarbon dating within the last ten years has provided a time-scale extending through all the Post-glacial and Late-glacial Periods, as well as the greater part of the time occupied by the last (Weichsel) glaciation. This has removed to some extent the obligation of palynology to provide a chronology for those times, although it may still serve this purpose in many situations when samples are too small or too contaminated, or are otherwise unsuitable for radiocarbon assay. Palynology largely returns, therefore, for deposits less than 50,000 years of age, to its prime function of revealing plant communities and ecological conditions at known stages of the past. For deposits, however, of greater age than this, notably the several interglacial periods, it retains its chronological or zoning function as no doubt our contributions will make clear.

The search for recognition of plant communities of the past is complicated, as we have said, by the fact that the growing deposit receives a pollen rain derived from a mosaic of natural communities in the surrounding landscape. A similar difficulty follows when we attempt to discern the pattern of the changes caused by plant and animal husbandry, for where forests have been cleared in such interest, the pollen of pasture, arable and fallow, is all incorporated together in the bog or lake deposits. Moreover, it may well be impossible to say whether a given ' clearance effect ' in the pollen diagram has been caused by a single large settlement near at hand, or by numerous smaller settlements widespread through the region.

We must furthermore take care not to assume that all communities of the past necessarily still exist today. Many assemblages of species in late Quaternary deposits, as for instance those of the Late-glacial Period in northwestern Europe, are aggregates that cannot be encountered in living plant communities, as witness the coining of the phrase ' Steppe-tundra ' to describe them. Nor need we expect that travel to the Arctic Circle will show the ecologist conditions fully comparable with those of the Late-glacial Period, if only because the latitude difference ensures such changes of length of day and intensity of insolation as operate independently of secular changes of climate.

We may on the other hand use our pollen analytic techniques to test the naturalness or permanence of certain communities that now seem almost certainly to be native and long-standing. Thus the ash woods of the older limestones of northern and western England have long been regarded as quite natural, but the careful pollen analyses recently made by Dr and Mrs Pigott in the Malham Moss, North Yorkshire, have yielded no trace of such woodlands though the analyses extend back as far as the Late-glacial Period and relict ash woods still clothe the neighbouring limestone scars.

These brief introductory remarks concluded, I may now say with what pleasure I look forward to hearing the conclusions of the work of several specialists each approaching study of Quaternary Ecology from his own particular angle. The holding of a Symposium such as this, and the excellent attendance, marks the substantial progress that our studies have now made, and we are grateful to the Society for having organized it.

2. PEAT STRATIGRAPHY AND BOG REGENERATION

By D. Walker

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Despite the fact that their vegetation must represent some of the most natural left in the British Isles, our knowledge of the dynamic ecology of bogs is very incomplete. By far the greatest area of bog in the British Isles belongs to the ' blanket bog ' type but more convenient units for study are the ' raised bogs ', the characteristic topography and vegetation of which present specially interesting problems (Tansley, 1939).

Only a relatively small proportion of our raised bogs seem to be actively regenerating at the present day. The surfaces of many are dominated by *Calluna vulgaris* or *Eriophorum vaginatum* and are scarred with erosion channels. Many others, particularly in Somerset, Lancashire, Cumberland and Ireland, are being drained and cut for fuel and litter. It is evident from the depths of peat which form these bogs—accumulations between six and ten metres are not uncommon—that conditions which are not conducive to peat accumulation have not been characteristic of them in the past. Indeed, the past two or three thousand years, usually represented by undecayed and unconsolidated peat, seems to have been a period of very active bog growth with species of *Sphagnum* occupying a very important role in the plant communities. It has therefore become customary to describe as ' living ' bogs those few which retain a surface vegetation rich in *Sphagna* with a water table very close to the surface, and which seem to be actively producing new peat by rapid upward growth. The edges of such a raised bog slope more or less steeply from marginal streams or fens and are relatively dry. The central area, however, is flat or only slightly sloping and is covered by a matrix of hummocks and hollows, many of the latter being flooded. Indeed in some cases more than half the surface might be open water containing islands or narrow meandering ridges of *Sphagnum*-dominated plant communities. If the central area of the bog is flat, hummocks and hollows seem to be randomly arranged, but where the surface is even slightly sloping the hollows are commonly oriented with their long axes along the contours of the slope (Plate 1).

Most theories of bog regeneration depend on assessments of the significance of this hummock and hollow system and attribute varied importance to the alignment of these features across the slope. Osvald (1923, 1949) described pool and hummock as genetically inter-related in a ' regeneration complex ', an idea also applied by Godwin and Conway (1939) at Tregaron. According to this theory, a pool is obliterated by *Sphagna* encroaching from neighbouring hummocks. The wet hollow so produced forms an ideal substratum for the establishment of rapidly growing, hummock-forming, *Sphagna* such as *S. papillosum*, *S. imbricatum* and *S. rubellum*, together with such flowering plants as *Rhyncospora alba*, *Erica tetralix*, *Narthecium ossifragum* and *Drosera rotundifolia*. From the hollow grows a hummock which, becoming drier at the top, is dominated by *Calluna vulgaris*. Upward growth is then considerably retarded and the ageing *Calluna* may become overgrown with lichens and, in drying, expose the hummock top to erosion, mainly by wind. Meanwhile, surrounding hollows have, in their turn, entered the phase of active hummock building and these young, growing, hummocks soon overtop the old eroding one and, shedding their water onto it, convert it to a pool. The cycle then begins again and the general mosaic of communities and topography on the bog surface is maintained whilst the conditions at any one point are continually changing. A difficulty in convincingly demonstrating this theory lies in the relative scarcity of old, eroding hummocks on most ' living ' raised bogs. This might be explained by supposing this stage to be very rapidly accomplished compared with the infilling of a pool or the upgrowth of a hummock, for it is undeniably difficult to recognize a hummock about to degenerate and a pool newly formed. A more likely explanation, and one suggested by Osvald himself (1923), is that hummocks rarely reach the fully mature stage when degeneration becomes inevitable but are reconverted to wet hollows as the younger hummocks around begin to overshadow them. This explanation, however, leaves the origin of the open water pools substantially unaccounted for, although they might be residual from Osvald's ' Teichkomplex ' ; relatively large areas of bog surface temporarily flooded by differential growth in different regions of a single bog. Pearsall (1956) interprets the aligned pools on a sloping bog surface as flooded hollows between pressure ridges developed where the downslope movements of the bog peat is impeded. This same movement accounts for other pools which are thought to have their origin in ruptures of bog surface under tension. Sjors (1948, 1950) has not offered an explanation of these phenomena although he points out that open water pools only exist where the water table is very close to the surface and that the presence of the pools allows the bog surface to receive much greater volumes of water than would otherwise be the case before erosion begins. In general pools are more frequent features of bog surfaces in more humid regions and may be considered as an oceanic facies of the raised bog formation.

The stratigraphy of the peat formed by actively growing raised bogs in the recent past should yield positive information about the mechanism of regeneration. Such data which have been used in support of the regeneration complex hypothesis seem to be drawn from records of single borings (Tansley, 1939 b) which leave the horizontal extent and relationships of the peat layers in doubt. Godwin and Conway (1939) showed by stratigraphic studies the pool and hummock complex at Tregaron to be very largely a young feature representing a rejuvenation of bog growth after a former standstill. Ratcliffe and Walker (1958) showed the hummock and hollow mosaic on the Snibe Bog in Scotland to be the first generation of this formation there and to have originated from a flatter, more uniform vegetation, probably in response to increased wetness of the bog. Walker and Walker (1960) have recorded the detailed stratigraphy of post-' Grenz ' peats in a number of Irish bogs exposed by peat-cutting. Areas of sections up to 5 metres long and 2 metres deep were accurately recorded and the communities from which the different peat types were derived were identified with greater or lesser success. In spite of the difficulty of identifying synchronous horizons, certain general conclusions emerged which are broadly confirmed by observations elsewhere, e.g. on the Solway mosses in Cumberland.

In the bog sections so far studied, remains of full cycle regeneration complex are very rare indeed. Occasionally, however, evidence of ‘ short cycle ’ regeneration complex is found in contexts where it is reasonably certain that neighbouring hummocks and hollows have been converted, the one to the other, each providing a source of new species for the other. It is difficult to understand why, at an intermediate stage, a more or less uniform community is not established, unless some periodicity in life history of the dominant plants or a control of water régime external to the bog itself is active. A common feature of all the stratigraphic evidence for any form of regeneration complex which has been recorded by these authors is the small size of the units involved, the distance between neighbouring hummock top and hollow bottom rarely having exceeded half a metre, even allowing for compression of the peat.

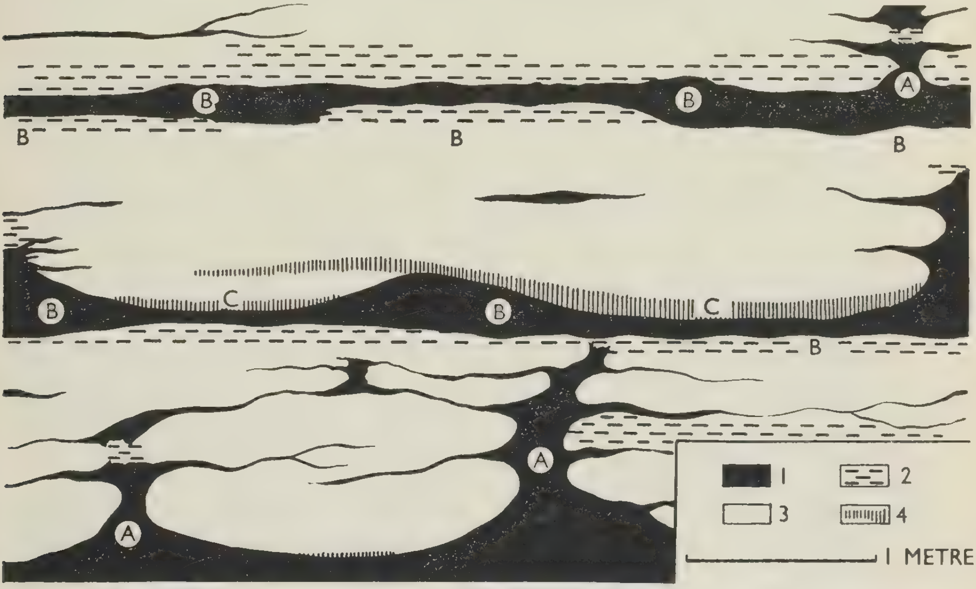

FIG. 1.—Diagrammatic representation of some common stratigraphic features in Irish bogs. 1, *Calluna-Sphagnum* peat, H 6–9. 2, *Sphagnum-Calluna* peat, H 5–7. 3, *Sphagnum* peat, H 2–4. 4, Pool mud and pool peat. A, Hummocks persisting and periodically spreading over neighbouring filling hollows. B, Uniform and widespread swards of vegetation. C, Large pools.

More often than not, however, when the stratigraphy shows a hummock to have matured, from an infilled pool or a level sward, it does not show any sign of autonomous deterioration at the top. Instead, it seems that, as surrounding infilling hollows reached the level of the hummock top or slightly below it, the hummock communities grew outwards, often producing small subsidiary hummocks over former hollows. Then, probably as a result of the changed water relations and the new availability of hummock-building species, the mature hummock was rejuvenated and grew upwards anew. This process may have been repeated for several ‘ generations ’ of hummock and would itself have perpetuated an over-all stable mosaic of communities, except that pools need never have been formed. The stratigraphy shows, however, that even the most strongly-growing hummocks sooner or later disappear, either by becoming the nuclei for the establishment of uniform, *Calluna*-dominated, sward, or by being overcome by *Sphagnum*-rich communities, also of relatively even topography (Fig. 1). No cyclic regeneration processes seem to be involved in these systems.

Evidence of former pools is found in the form of layers of plastic mud, often containing the remains of algae and invariably rich in *Sphagnum cuspidatum*. Occasionally the relics of small pools, of the order of a metre across, are found, but much larger deposits, three to six metres in section, are much more common. In any bog there is a tendency for these pools to occur at a few, fairly distinct, levels in the peat. These pool muds usually overlie peats of mature hummock or sward communities ; peats rich in *Calluna vulgaris* with *Eriophorum vaginatum*, *Sphagnum imbricatum* and *S. rubellum*. That these pools did not belong to the usually accepted regeneration complex cycle is clear from the facts that they did not necessarily lie above hummock peat and that, when they did so, they also transgressed the hollows between. Laterally the pool muds are usually bounded by particularly high and persistent hummocks. It is difficult to be certain that these pools did not arise after surface movement of the peat or erosion of some kind. No positive evidence of these has been found, however, and they are thought not to have contributed substantially to pool formation. The infilling of these pools was usually accompanied in its late stages by the overgrowth of the marginal hummocks and the development of a fairly uniform sward or, more rarely, a short-cycle regeneration complex. These large pools, which are almost certainly to be compared with the large pools on modern bog surfaces, have usually formed over mature surfaces during periods of rejuvenated peat accumulation. They seem not to be local phenomena initiated by cyclical vegetational changes but to depend on a general change in hydrography of the bog as a whole. They are similar in kind to, but different in scale from, the recurrence surfaces (Granlund, 1932, Overbeck & Griéz, 1954, Godwin, 1954, Olausson, 1957).

If it is correct to identify these pool muds as the fossil remains of pools similar to the large pools on modern bog surfaces, then it seems most unlikely that the latter are erosional features or that they are stages in a self-perpetuating regeneration complex. Their origin during the rejuvenated growth of a bog is consistent with the findings at Tregaron (Godwin & Conway, 1939) and the Silver Flowe (Ratcliffe & Walker, 1958). These large pools are not necessarily genetically linked to the small hollows which may form part of a short-cycle regeneration complex. The reason for their orientation is still obscure, but their divorce from the random small hollows gives support to a modification of Pearsall's pressure-ridge explanation if this is applied to a developing situation on a growing surface and not to positive movement of a formed surface.

The conclusion is tentatively reached that neither the small scale, short-cycle, regeneration complex nor the larger pool system is self-perpetuating and independent of the hydrology of the bog as a whole. After one or two generations of either, a uniform sward of vegetation is usually established and remains for some time, growing upwards until an entirely new period of hummock and hollow formation begins. These uniform sward communities seem to have had much in common with the older pre-' Grenze ' peat formers. They might well represent the normal bog communities under relatively stable or slowly changing climatic conditions, whereas the younger pool and hummock communities of various kinds are a reaction to climatic conditions of a different kind, an idea implicit in much of Conway's (1948) discussion. Naturally, the change from one vegetation-topography type to another will depend not solely on the climate but also on the geography and previous history of each bog itself. It may be that pool and hummock systems allow bogs to achieve greater vertical height but they also expose them to greater erosion risks from the large volumes of free water so precariously damned on their surfaces. The pool and hummock systems may not result in more rapid over-all growth of peat, for radiocarbon dates accumulated from a number of sites in Europe suggest a mean aggradation rate of the order of 1 cm. in 20 years for both pre-Grenze and post-Grenz peats.

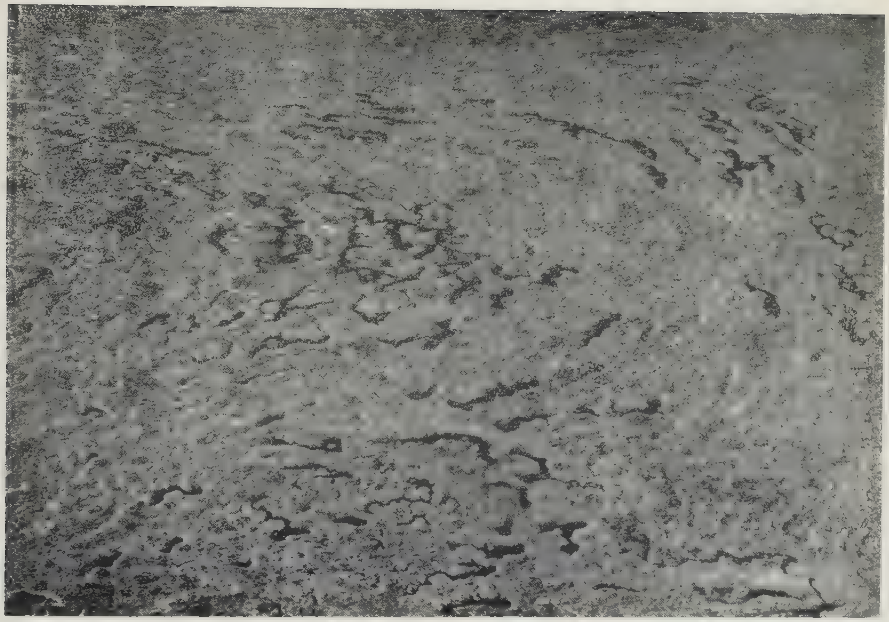

PLATE 1.—Aerial photograph of a part of the Silver Flowe bog, Galloway, Scotland, showing the distribution of pools and hummocks. (Phot. J. K. St. Joseph. Crown Copyright Reserved.)

The over-all impression, therefore, is that our 'living' bogs of the present day are relatively unstable features, vegetationally and geographically, which are very susceptible to climatic change but which, under constant climatic conditions, would probably develop in the direction of a reduction in the number of pools and the establishment of fairly uniform plant communities.

It is a pleasure to thank my wife and all my colleages and friends with whom I have discussed these topics. The aerial photograph in Plate 1 was supplied by the Curator in Aerial Photography of Cambridge University.

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3. POST-ATLANTIC FORESTS IN IRELAND

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I. INTRODUCTION

THE work of the earlier Quaternary botanists, such as Clement Reid, was concerned with identification of macrofossils from sites of geological or archaeological interest and making inferences of a rather general character about climate and habitat from the species determined. This method was limited in value because, with few exceptions, Quaternary plant macrofossils are unsuitable for dating purposes, and there was no satisfactory chronological basis for comparing fossil floras. The introduction of pollen analysis provided a suitable method for subdividing the Late-Glacial and Post Glacial periods into zones. The pollen-zones are defined by major changes in composition of the pollen-rain, which themselves reflect vegetational change. The assumption is made that zone-boundaries are contemporaneous over wide areas because large scale vegetational changes must have climatic causes which would have simultaneous effects over great regions. Recently the invention of radio-carbon dating has made it possible to test this assumption and has on the whole confirmed it. The Post-Atlantic period in Ireland is difficult to zone because of the lack of strongly-marked climatic effects and because man had begun to affect the pollen rain by selective forest clearance, so that it is often difficult to decide whether a particular change is climatic or caused by man. However we can detect a consistent series of events in our pollen-diagrams. Because of the regularity and uniformity with which these occur it is a reasonable hypothesis to assume them to be contemporaneous all over the country. This implies that the changes we record are either determined by natural events, or, if man-caused, reflect a marked impact on natural vegetation due to the introduction over a short period of a new form of agriculture. Radio-carbon dating has made it possible to test this hypothesis and has supported it. The first part of my paper describes the pollen-zones established for the Post-Atlantic in the Central Plain of Ireland and their absolute age as determined by radio-carbon dating.

The approach to Quaternary studies so far outlined is a geological one, in that one is concerned with establishing chronology and characterizing the fossil assemblages of particular periods. It is an essential preliminary to more purely palaeo-ecological studies which can hardly be carried out except within a thoroughly satisfactory chronological framework. Naturally much information of interest to ecologists, particularly autecologists, arises from Quaternary studies, but they are of limited interest to synecologists because fossil vegetation of dry land is treated as a whole and plant communities (the ' noda ' of Poore, 1955) are not effectively distinguished. Pollen-analysis gives little synecological information because pollen rain gives no direct evidence of the quantitative relations of trees, which are the major pollen producers, nor of the patterns in which they are organized. The difficulty is that pollen-rain, which cannot be measured absolutely, may be derived from a considerable area around the sampling-point and many different plant communities may contribute to it. Some pollen travels great distances ; for example, pollen of *Fagus* and *Tilia*, both non-native trees, appears regularly in Irish bogs in small quantity. In addition some tree species produce pollen in great quantities, while others produce much less from stands of comparable area. (Faegri & Iversen, 1950, discuss these problems fully.) In spite of these difficulties there may be a possibility of using the data of pollen-diagrams to distinguish ' noda ' within Post-glacial forest vegetation. This is discussed in the second part of the paper.

2. Post-Atlantic Pollen-Zones from the Central Plain of Ireland

I describe below in an abbreviated form the features used to zone the Post-Atlantic period. Nomenclature, and the zone-boundaries with minor modifications follow Mitchell (1956) whose pollen diagrams may be used to illustrate the features described. (See especially the diagrams from Leigh, Agher & Clonsast, B.) The fossil pollen of the period consists largely of *Corylus*, *Alnus*, *Betula*, *Pinus*, *Quercus*, *Ulmus* and *Fraxinus* with varying proportions of herbs and small quantities of shrub pollen. The behaviour of *Ulmus* and *Fraxinus* is of most importance for chronology. In the description ' increases ' and ' decreases ' of tree species refers to their percentage contribution to the pollen rain. The absolute dates are each based on at least three radio-carbon dates from different bogs in Ireland, except for the Zone VIII middle-upper boundary which is based on two, and Zone IX–X for which the historical date is known.

Zone VII–VIII lower, 3100 B.C. Transition from Atlantic to Pagan period. The zone boundary is marked by an abrupt decrease in *Ulmus*, sometimes from 20 per cent to 1 per cent of the tree pollen in a few centimetres of sediment. Simultaneously there is a fleeting appearance of *Plantago lanceolata*. Later *Ulmus* almost recovers its former values.

Zone VIII lower-middle. 2400 B.C. *Fraxinus*, previously very sporadic, begins to make a steady contribution to the pollen rain. At about the same time *Ulmus* decreases permanently in quantity. *Plantago lanceolata* is frequent from this time on. *Pinus* becomes extinct over much of the Central Plain in the middle of this period.

Zone VIII middle-upper. 300 B.C. *Fraxinus* increases substantially in abundance, doubling its former values. Its behaviour relative to *Ulmus* shows that any factor which affects one affects both, so one may assume them to have been associated in a distinctive plant community. In this period *Fraxinus* has values up to 12 per cent of tree pollen, a much larger proportion than is found elsewhere, but not surprising when one considers that it is now a very common tree of calcareous regions in Ireland.

Zone VIII upper-IX. A.D. 250. Transition from Pagan to Christian period. *Fraxinus* decreases greatly in abundance and *Ulmus* becomes very rare or actually disappears. There is a great increase in *Betula* and *Alnus*. After A.D. 500 pollen of the weed *Artemisia* appears continuously in quantity, having been rare before.

Zone IX–X. A.D. 1700. Transition from Christian to Afforestation period. About the end of the seventeenth century planting of exotic trees took place on estates. This is reflected in the appearance of much pollen of *Pinus, Fagus* and *Ulmus* in the top few centimetres of our bogs.

The cause of the *Ulmus* fall at 3100 B.C. may be the activity of prehistoric farmers. We know from radio-carbon dates that people of the Western Neolithic culture were in north-east Ireland at that time, though not necessarily in the Central Plain. The argument is that *Ulmus*, as a suitable fodder crop growing on the best soils for agricultural purposes would be cleared first with the subsequent appearance of such pasture plants as *Plantago*. (See Iversen (1941), Troels-Smith (1953, 1955) and Mitchell (1956) for detailed argument.) This explanation does not adequately explain all the evidence. We must note first the enormous forest destruction which a fall from 20 per cent to 1 per cent in *Ulmus* represents. The fall appears to be synchronous throughout north-west Europe (van Zeist, 1959, Giot, 1959). This would imply a very large-scale immigration into Ireland over a rather short period. The difficulty of transporting large numbers of people and their domestic animals across the sea to Ireland and the rather small Mesolithic population (Movius, 1942) would have made a rapid build-up of population unlikely. Even if the Western Neolithic people could arrive in substantial numbers in a short period, did their economy demand forest destruction on such a scale, and how is one to explain the recovery of *Ulmus* to nearly its former frequency ? A more satisfying explanation, hinted at by Aletsee (1959) is the possibility of widespread elm disease. Small numbers of farmers could have moved into areas cleared by disease and pasture weeds would have spread with them. Later, with the recovery of the elms, the cleared areas became forest once more, the weeds disappeared and the small population would have been restricted once more to thinly forested upland or coastal regions. After 2400 B.C. the evidence of the pollen-diagrams indicates unambiguously that widespread forest clearance was in progress.

The Zone VIII–IX boundary is marked by reduction in the pollen of both *Ulmus* and *Fraxinus*. This is probably due to forest clearance from calcareous soils. The clearance is not comparable to the earlier elm fall because two species are clearly involved and their reduction is permanent. One must also consider that at this time the population was more numerous, and was equipped with metal tools, and that the total forest area had probably been greatly reduced. The A.D. 250 clearances may be evidence of a new type of rural economy being introduced under the influence of neighbouring Roman Britain, in which tillage and fixed settlement played a larger role than before.

There is little evidence of major climatic change from Ireland for the Post-Atlantic period. The great increase of *Fraxinus* about 300 B.C. may well reflect climatic change, at least there is no other obvious cause. In several areas the beginning of blanket-bog growth may be accurately dated to about 2000 B.C., either by direct radio-carbon dating or by knowing, ultimately on the evidence of radio-carbon dates, the age of archaeological objects or structures buried by peat. For example, at Carrowkeel Mountain tombs of the Boyne culture datable to about 2200 B.C. are peat-buried. On the same mountain a stone wrist-bracer of Beaker age, dating to shortly after 2000 B.C., was found, a few centimetres from the base of the bog. One may suppose that the bog began to form shortly before 2000 B.C. This evidence shows that the climate was favourable for peat formation by 2000 B.C., but does not exclude the possibility that this condition had existed for some time before. The actual beginning of peat formation at any one site may have been accelerated by forest destruction and soil impoverishment due to primitive farming practices, or it may have been the culmination of a long period of soil impoverishment by natural agencies. To conclude, there appears to be some not very satisfactory evidence for climatic change, first shortly before 2000 B.C. when blanket-bog formation began in several areas ; second, about 300 B.C. when the substantial increase of *Fraxinus* may indicate a change, perhaps in the direction of a more oceanic climate.[1]

3. Obtaining Ecological Information from Pollen-diagrams

The difficulties mentioned in the introduction make it impossible to extract much synecological information from a single pollen-diagram. If however one can obtain a pollen-diagram from an area which forms a very distinctive habitat and compare it with a diagram from an adjacent contrasting habitat some progress can be made. (Table I illustrates the kind of difference there may be between pollen spectra from very different habitats.) It is essential that the diagrams should come from sediments in small steep-sided basins, (to avoid effects of marginal fen-woods), which are surrounded in every direction by as

Table I

	(1) Tullymackan, Co. Galway	(2) Killarney, Co. Kerry	(3) Agher, Co. Meath
Alnus	6·6	7·0	10·0
Betula	3·6	34·6	2·0
Pinus	1·3	5·6	...
Quercus	3·0	39·3	11·0
Ulmus	2·3	1·3	4·5
Corylus	74·6	9·6	61·0
Fraxinus	8·3	2·3	11·5
Hedera	0·6	4·0	0·5
Ilex	...	9·0	1·0
Taxus	3·0	2·0	0·3
Arbutus	...	1·0	...

Pollen spectra from zone VIII upper from various habitats. (1) A Carboniferous limestone region. (2) An acid Old Red Sandstone region. (3) Central Plain boulder-clays. Pollen of *Hedera, Ilex, Taxus* and *Arbutus* is excluded from the pollen sum.

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[1] It is hoped to publish these arguments in detailed form in *Proceedings of the Royal Irish Academy*.

uniform a habitat as possible for at least 1 km. This ensures that as much as possible of the pollen rain is being produced from a rather uniform type of vegetation. The most satisfactory type of region for study is one which shows gross geological contrasts. Such a region lies between Lisdoonvarna and Lough Graney in County Clare. In a strip of country some 35 km. from west to east and 15 km. north to south the following contrasting habitats occur, passing from west to east. 1. Carboniferous shale hills, no drift cover, largely a blanket-bog region. Some *Quercus sessiliflora* woods. 2. Bare limestone pavement, little or no drift, vegetation of *Corylus* scrub with sparse *Fraxinus* and *Ulmus*. *Quercus* and *Alnus* totally absent. 3. A drumlin belt, heavy calcareous clays, now all farmed. 4. Drift-free Old Red Sandstone with blanket bog and some *Quercus sessiliflora* woods. It is possible to find suitable small basins for study within each habitat type. Eventually it is hoped to produce a closely spaced grid of pollen-diagrams for the whole strip. One may anticipate that large pollen-rain differences will be found on crossing habitat boundaries and that these differences, reinforced by macrofossil studies, can be used to determine at least which species, or combination of species, grew in a particular habitat at any period.

To evaluate comparisons of fossil pollen rain from different sites it is necessay to study the modern pollen rain of well-characterized woodland noda by collecting surface samples from, for example, moss patches. It is possible from such studies to see the kind of variation which is found in modern pollen rain and how it is related to the composition of nearby woodland. It is also important to study, in regions of natural woodland, the changes in pollen rain which occur when one crosses a major geological boundary. The purpose is to find out over how great a distance pollen from adjoining communities intermingles to any great extent, so that in setting out to study a fossil community one knows how big an area of uniform habitat around the sampling point is necessary if influences from neighbouring communities are to be avoided. Further, for the same reasons, one needs more information about how far the bulk of the pollen of a given species travels from its parent tree. There are good opportunities to study this in Western Ireland where wooded islands exist in lakes surrounded by great expanses of blanket-bog. The pollen carriage can be studied by taking surface pollen samples at intervals from the dispersal point and relating the frequency of the pollen of trees from the islands to some relatively abundant pollen, such as *Pinus*, which is far-travelled and therefore evenly distributed.

In conclusion I would like to point to two defects in our information which hamper the interpretation of fossil finds. First there is a lack of autecological information, (which is being remedied by the Biological Flora), particularly of precise information about climatic tolerances of species, allowing for the fact that different populations of the same species will vary in this respect. It is possible at present for very varying opinions to be held about the climates of the various interglacial periods because of the lack of precise information about the climatic implications of fossil finds. This situation could be clarified experimentally by the use of ' ecological machines ' (Clapham, 1956) for a few critical cases. One would like to know, for example, the temperature ranges within which some aquatic species often found fossil will (a) grow vegetatively (b) fruit ; or, for example, whether Iversen's (1954) deductions about the Late-Glacial climate could be verified experimentally. Failing experimental data it will continue to be extremely difficult to produce satisfactory evidence for climatic change in the Atlantic and Post-Atlantic periods. Secondly, there seems to be a possibility, (see Heslop-Harrison, 1957) that wide-ranging species may have pollen production which varies according to the climate in which they are growing. This would give rise to difficulties in comparing pollen-diagrams from different regions. Clearly the recent advances in the study of the physiology of flowering will be of great importance in Quaternary botany.

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4. THE ATLANTIC—SUB-BOREAL TRANSITION

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THE diagram (Fig. 1) has been drawn up to illustrate some of the points to be discussed. An attempt has been made to depict the most common trends of certain pollen curves in the middle of the Post-glacial period at some north-west European sites. Curves are given for *Ulmus*, *Tilia*, *Fraxinus* (omitted for S.W. Norway) and *Hedera*. Histograms are given for *Hedera*, *Ilex* and *Viscum*. The *Hedera* histogram for England is based on incomplete data (Godwin, 1956) and no histogram is given for *Ilex*.

Letter symbols are used to indicate levels at which there is evidence for human activity, and levels at which pollen of *Plantago lanceolata* occurs ; a key to these symbols is given in the diagram.

Little attempt has been made to represent the actual values of the curves and histograms, since the pattern of the pollen curves is more important than the actual percentages. The fact that certain similar features are drawn at the same level does not necessarily imply that the features are contemporaneous, except in so far as it seems likely, from radio-carbon dating of a rather small number of sites, that the decline of the *Ulmus* curve might prove to be broadly synchronous.

The decline of the *Ulmus* curve is, of course, the outstanding feature of the transition between the Atlantic and Sub-boreal periods throughout north-western Europe. In the British Isles the decline of the elm curve is used to define the Atlantic/Sub-boreal zone boundary. Godwin (1956 : 99) has pointed out that in the English pollen diagrams, the *Tilia* curve tends to decline at the same time as the *Ulmus* curve, particularly in the north. Godwin considers that there was probably a climatic change at the Atlantic/Sub-boreal boundary. But Mitchell (1956 : 235) has posed the question ' is it possible to speak of some climatic deterioration that made conditions less favourable for *Ulmus* throughout north-west Europe ? ' in view of the recovery of the *Ulmus* curve in many Irish diagrams.

The concept that the Sub-boreal period was warm and dry has been questioned by both Godwin and Mitchell. Godwin considers that the climatic optimum probably extended from late Boreal time up to the end of the Atlantic period, and that the decline of elm and ivy, and the increase of ash, at the Zone VIIa—VIIb boundary probably mark a cooling of climate (Godwin, 1956 : 339, etc.).

Jessen (1949 : 258–261) considered that in Ireland the climatic optimum fell in the Sub-boreal period largely because of the high levels of the *Quercus* curve. Mitchell later questioned this idea. He considered that while optimum conditions for *Quercus* might have occurred in the Irish Sub-boreal, this is too narrow a definition for the climatic optimum (1956 : 198–199). In 1956 Mitchell ceased to use the term Sub-boreal for Irish deposits.

Godwin has pointed out that the importance of dry bog-surfaces and tree layers at the end of the Sub-boreal tends to be over-emphasized by the unhumified nature of the deposits overlying them. The important point here is that there is little sign in British peats of a sudden change towards drier conditions at the end of Atlantic time. Indeed, in dealing with the Pennine blanket peats Conway (1954 : 139–141) found that there was often a change, near the level of the *Ulmus* decline, from an amorphous highly humified peat to a peat rich in *Sphagnum* leaves. A similar stratigraphical change is even more pronounced at the Atlantic/Sub-boreal boundary at Hatfield Moors, in south-west Yorkshire (Smith, 1958 a). Conway has pointed out that the stratigraphical change is either a natural developmental stage in the growth of the bog or it is a response to a climatic shift. The second alternative would imply a change towards wetter conditions. Both Conway and Mitchell (1951 : 198) have considered that, because of the marked rise of the alder pollen curve at the end of the Atlantic period, it is difficult to consider that the Sub-boreal was drier than the Atlantic period. In Ireland, this rise of the *Alnus* curve is often short lived, and associated with the first temporary decline of the *Ulmus* curve. It is difficult, therefore, to tell whether the rise of the *Alnus* curve represents an actual increase of alder or whether it was due to decreased amounts of other pollen types.

Van Zeist (1959) considers that where one is dealing with *Ulmus glabra* and there is no decline of *Hedera* then ' a climatic factor can hardly be held responsible for the decline of *Ulmus*.' He maintains that a climatic deterioration is not likely to have affected elm without also affecting ivy. Van Zeist extends his conclusion to Holland, but we can hardly suppose that, there, *Ulmus glabra* was the only species. Because of the apparent contemporaneity of the *Ulmus* decline in N.W. Europe, as shown by radio-carbon dating, Van Zeist comes to the conclusion that ' although the *Ulmus* decline cannot be credited to a climatological cause, it still marks a change in climate.' He maintains that if this were not the case then it would be difficult to explain the decrease of *Hedera* which takes place simultaneously in some areas.

The decline of *Hedera* in the Danish diagrams is one of the features used by Iversen to define the Atlantic/Sub-boreal boundary. In Denmark the decline of *Hedera* is seen in a pollen curve. In other areas, however, because of the scarcity of *Hedera* pollen, histograms have been drawn up showing, for each sub-zone, a value for *Hedera* pollen as a percentage of the total tree pollen found in a number of diagrams. There is, of course, a danger of circular argument in basing conclusions on the histograms, for we cannot be sure that the frequency changed at the zone boundary. Iversen (1944) has shown by direct observation and by his ' thermal limit ' curves that *Hedera* is susceptible to winter cold, and that it does not grow normally, where the mean January temperature is below −1·5° C. except in particularly favourable local conditions. He suggests that the decline of the *Hedera* curve at the Atlantic/Sub-boreal boundary in Denmark indicates a lowering of winter temperature. Iversen estimates that the mean January temperature fell from about +0·5° to −1·0° C. His calculations from the occurrence of *Viscum* pollen show that the mean July temperature in the Sub-boreal period was about 2° C. higher than at present, and that in the Atlantic period it was at least 1·5° C. higher than at present. These figures are generally regarded as agreeing fairly well with the classical concept that there was an increase of continentality between the Atlantic and Sub-boreal periods. In Denmark the frequency of *Viscum* pollen is lower in the Sub-boreal than in the Atlantic period ; but Iversen has not argued from this that a change of summer temperature took place at the zone boundary.

Degerbol and Krog (1951) have shown that the European pond tortoise (*Emys orbicularis*) was present in eastern Denmark in both Atlantic and Sub-boreal time. A high summer temperature is required for the success of this species and the evidence indicates a summer temperature at least 2° C. higher than at present. In spite of the fact that the distribution of *Emys* is not entirely dependent on a high summer temperature, one might have expected that, if there had been an increase of summer temperature in the Sub-boreal period, the species would have shown an increased westerly distribution. But in fact the reverse seems to have been the case. This kind of argument, however, cannot be regarded as conclusive.

Jessen (1949) regarded the increased frequency of *Hedera* and *Ilex* pollen in his Irish Sub-boreal period as indicating that higher summer temperatures favoured these species while, in this oceanic area, they were not affected by lower winter temperature.

Now on a superficial examination, Mitchell's new zone boundary VII–VIII (Mitchell, 1956) (*i.e.* the boundary between his Atlantic and Pagan periods) appears to be equivalent to Jessen's zone boundary VIIa–VIIb (Atlantic/Sub-boreal) (Jessen, 1949), since they both depend on the decline of the *Ulmus* curve. In point of fact, in those diagrams that he has re-zoned, Mitchell's new zone boundary is markedly lower than Jessen's. But in other diagrams, such as Cloughmills, Mitchell's zone boundary would be quite close to Jessen's. These facts (and other considerations) might affect the *Hedera* and *Ilex* histograms if the frequencies were recalculated using Mitchell's (1956) zone scheme. Of his more recent Irish pollen diagrams, Mitchell (1956) has stated that, though the amount of evidence is limited, it suggests that there was no significant variation in the amount of *Hedera* pollen reaching the bog surfaces in the Post-Boreal period.

In western Norway, Faegri (1940, 1944) regards the Sub-boreal period as the time of the climatic optimum because of the increased values for the mixed oak forest constituents. He points out particularly, the higher values for the *Tilia* curve and the increased frequency of *Hedera* pollen in the Sub-boreal period. Both these species appear now to be restricted in their Norwegian distribution by the low summer temperatures. Faegri considers the first decline of the *Ulmus* curve in his zone X (Sub-boreal) to have been climatically conditioned, largely because there is little or no evidence of human activity. He admits, however, that it is difficult to imagine how climatic control operated. He points out that it cannot be assumed that a southern species of elm was involved, such as Iversen (1941 : 36) has suggested was the case in Denmark.

In the Oslo region, Hafsten (1956 : 90) considers that the climatic optimum occurred in the Atlantic period, (Zone VII in 1956, Zones VI and VII in 1957) mainly because of the greater frequencies of *Viscum* and *Hedera* pollen. He considers that the late expansion of *Tilia*, midway through the Atlantic period was probably due to a slight increase of continentality. This view is supported to some extent by the decreased frequency of *Hedera* and increased frequency of *Viscum* pollen.

Hafsten maintains that *Tilia* is dependent on high summer temperatures. He rejects arguments based on a slower migration rate for *Tilia* (cf. Firbas, 1949; Godwin, 1956: 183). While Godwin (1956) has not rejected the possibility that *Tilia* expanded late in the Boreal period because of a slow migration rate, he takes the view that in the English Post-glacial *Tilia* was behaving as our most warmth demanding tree. Hafsten's argument is based on the fact that *Tilia cordata* has a more southerly limit than *Ulmus glabra* in north-western Europe, but the reverse is true of Finland and Russia. But we must, however, always bear in mind Salisbury's warning (1926: 232) that 'mere correspondence of the limits of distribution of a species or community with climatic limits is at best presumptive evidence and no proof of any causal connection between them.'

In the north of England, recently investigated sites all show a late expansion of *Tilia*, after the expansion of *Alnus*, a feature similar to the behaviour of *Tilia* in the Oslo region. (Windermere, Pennington, 1947; Skelsmergh and Kentmere, Walker 1955; S.W. Westmorland, Smith, 1958 b, 1959; Scaleby, Godwin, Walker & Willis, 1956; Broadgate Fell, Blackburn, 1953; Stump Cross, Walker, 1956.) This fact might be explained on the basis that the temperature requirements of *Tilia* were not met in the north of England until early in the Atlantic period. But evidence such as finds of *Najas marina*, with its marked southerly Scandinavian distribution, from Boreal time, as far north as the Lake District (Walker, 1955), would seem to imply that summer temperature was not limiting the first expansion of *Tilia*.

It is not impossible, however, that the lower values for *Tilia* pollen in the Sub-boreal are due to a decrease of summer warmth. A decline of the *Tilia* curve at the Atlantic/Sub-boreal boundary is less marked in the south of England; a feature which is particularly noticeable in the diagrams from Hockham Mere, Norfolk (Godwin & Tallentire, 1951). It might well be that in the south of England *Tilia* was not affected because the temperature did not fall to a critical level. Clearly the effect of a climatic change will always depend on the pre-existing climatic conditions in any particular area. The fact that particular changes are not synchronous, or are restricted to a particular region, does not exclude a climatic explanation.

The difficulties of relating climatic factors to pollen curves are even greater in the case of *Ulmus* than with *Tilia*. Our continental colleagues assume in many cases the use of elm leaves and branches as fodder, and close to the *Ulmus* decline of the Atlantic/Sub-boreal transition very often there appear the first signs of the development of pasture and cultivation.

Van Zeist (1959) has rejected the suggestion put forward by Godwin (1956) that the *Ulmus* decline might possibly be due to the prevention of seed formation, by an increase in the frequency of late frosts. Van Zeist points out that *Fraxinus*, which usually increases as *Ulmus* declines, is also susceptible to late frosts. But, aside from any other considerations, it would seem equally likely that, before its expansion in the Sub-boreal period, ash was limited not so much by climate as by competition from elm for the damp deep calcareous soils. And the fact that ash has apparently been favoured by agricultural practices, (cf. Godwin, 1956: 157; Mitchell, 1956; Smith, 1958 c etc.) might be explicable on the grounds that on suitable soil this light-requiring species would have been able to establish itself in clearings.

Probably the greatest difficulty English workers have in accepting that the *Ulmus* decline was due to human activity is that pollen of *Plantago lanceolata*, one of the most generally accepted indicators of prehistoric agriculture, particularly of pasture, often occurs before the Zone VIIa–VIIb boundary. It seems unlikely that the finds of *Plantago lanceolata* pollen before the end of the Atlantic period can be all ascribed to contamination. By 1956 Godwin had recorded three Late-glacial finds and three Atlantic finds, and these records have recently been augmented by further finds in the Lake District (Smith, 1958 b, 1959) and Scotland (Donner, 1957). Godwin (1956) has taken the view that the early finds of *Plantago lanceolata* pollen may indicate that this plant did not enter the country with the first farmers, as in Denmark, but that it may have been present in this country before that time. This possibility means that it is difficult to know, in England, when *Plantago lanceolata* pollen is an indicator of prehistoric agriculture and when it is not.

So far, no examples of well marked forest clearance phases have been fully published for English sites comparable with the Danish ' landnam ' phases (Iversen, 1941, 1949). In several Irish pollen diagrams, however, it seems that we may well be dealing with roughly the same kind of ' clearance phase ' that Iversen has described. (*cf.* Corlona, Van Zeist, 1955 a ; Mitchell's diagrams, 1956 ; Fallahogy, Smith, 1958 c ; Parkmore, Morrison, 1959.) A curious feature of the Irish ' clearance phases ' is that while the *Ulmus* curve falls the *Quercus* curve does not. Mitchell (1956 : 235) has suggested that prehistoric man may have found that where elm grew most freely the soils were most suitable for his method of agriculture.

While he has not considered explanations other than human activity, Morrison (1959) has pointed out that we cannot distinguish between the possibility that elm was growing on the better soils, as association segregates, and the possibility of selective utilization ; either selective felling of elm, or use of the branches as cattle fodder, such as Troels Smith (1953) has suggested for some Danish and Swiss sites. At the moment we cannot distinguish between pollen of *Quercus petraea* and *Quercus robur*, but Morrison points out that if *Q. petraea* were the most usual species, then we might be justified in assuming that *Ulmus* was growing on the more fertile soils. On the other hand, if there was a proportion of *Q. robur*, it would probably have been competing with *Ulmus* for the better soils and the woodland would perhaps have been to some extent mixed.

Morrison takes the view that since, generally, the curves for all the mixed oak forest trees fall in the Danish ' Landnam ' phases we have evidence that the forest was in fact, truly mixed. On the other hand, Iversen (1949 : 10), in arguing against a climatic interpretation of the ' landnam ' phases has pointed out that ' here a lime forest, there an oak forest perished '. This conclusion no doubt includes the evidence from Mogetorp in Sweden, where it is largely the *Tilia* curve that declines. A similar conclusion has been reached by Van Zeist. In his diagram from Bargeroosterveld, in the province of Drenthe, the values for *Tilia* are much higher than in the diagrams from Emmen a few miles away (van Zeist, 1955 b). Van Zeist concludes that the forest near Bargeroosterveld must have been rich in lime trees and that perhaps lime was dominant. It appears then, that on the continent, the concept of a truly mixed deciduous woodland is being modified.

Oversen has argued against a climatic explanation of the Danish ' Landnam ' phases, but in Ireland, we cannot be sure that there was not a temporary climatic deterioration. For at one or two sites there is a temporary decline of the *Ulmus* curve with no indications of agricultural activity (*cf.* Dromsallagh, Mitchell, 1956). It is possible, however, that had more pollen been counted in these cases, some pollen indicative of agricultural activity would have been found.

Nor can we rule out the possibility mentioned by Watts (in this symposium) that in Ireland the decline of elm was due to disease. The apparent rapid recovery of the elm, and the often simultaneous decline of pine would, however, appear to argue against it. But these are not strong arguments for we cannot estimate how long it would have taken for the elm pollen production to regain its former level, because, aside from any other considerations, the resurgence of elm after its (putative) destruction by disease might have been due both to recovery of injured trees and the spread of resistant types. It is also true, of course, that diseases are not necessarily specific. Professor J. Heslop Harrison has drawn my attention to the recent spread of ' die back ' of *Betula lutea* to *Betula papyrifera* and even *Acer saccharina* in the Boreal forest of eastern Canada. Clark & Barter (1958) maintain that the ' die back ' is due to a virus, but it is not impossible that some physiological factor, perhaps related to climatic conditions, has played some part, at least in the spread of this catastrophic disease.

The acceptance of disease as largely responsible for the *Ulmus* decline in Ireland would not exclude the action of other factors. This becomes particularly clear when we consider that disease might have been spread by animals, particularly insects ; just as today the Dutch elm disease (*Ceratostomella ulmi*) is mainly spread by the elm bark beetles (*Scolytus* spp.) and, in North America, the virus causing phloem necrosis in elm is transmitted by an elm leafhopper (e.g. *Scaphoideus luteolus*) (May & Baker, 1952). Indeed, the spread of an insect vector in a number of successively favourable years would offer an explanation of how a minor short-term ' climatic ' change might, indirectly, have had an effect on the elm disproportionate to its severity. Equally, of course, the dispersal or germination of fungal spores, or the dispersal of a parasitic insect, might have been favoured by a short-term ' climatic ' change.

The intensification of the prevalence of disease by the activities of man is another possibility. We might quote the example described by Keen (1952) of the increase in the numbers of certain bark beetles (in this case not elm bark beetles) because they had been able to breed freely in trees killed or damaged by fire. Indeed, it seems likely that any increase of dead wood, such as felling or severe storms might have produced, might have given rise to an increased insect population. This kind of example could, of course, be multiplied, and I have given them merely as a plea for thinking in terms of the interaction of numerous biological factors. It is not intended to imply that there is any evidence that any of these processes have operated at the *Ulmus* decline.

Even if we discount the possibility that the actual decline of *Ulmus* was due to human activity we shall still have to explain the expansion of *Plantago lanceolata* and other weeds. It is true, however, that in Ireland, as in England, pollen of *Plantago lanceolata* is found before the marked rise of the curve at the *Ulmus* decline (*cf.* Fallahogy, Smith, 1958 c ; Parkmore, Morrison, 1959 ; Newferry, Smith, unpublished) but there are no records from the Late-glacial period. We certainly need more unequivocal correlations between early Neolithic settlements and the pollen record before a proper attempt can be made to understand the problem. So far the only reasonably firm correlation with the *Ulmus* decline is the sherd of pottery ' of the Neolithic "A" family ' from Dunshauglin (Mitchell, 1940, 1951), and here, unfortunately, full pollen analyses have not been made.

While Watts may be correct in assuming that the decline of the *Ulmus* curve represents a catastrophic reduction of elm that could not have been produced by the activities of a small Neolithic population, we must bear in mind the argument used by Mikkelsen (1949). Mikkelsen considers that during the ' land occupation phases ' in some of his Danish diagrams, *Alnus* and *Betula* replaced *Quercus*, whose curve shows a marked decline ; he argues that since *Alnus* and *Betula* produce more pollen than *Quercus*, a slight decrease of *Quercus* in the forest appears as a marked fall of the *Quercus* curve in the pollen diagrams.

It has been pointed out that the *Alnus* curve usually rises temporarily at the first *Ulmus* decline in the Irish diagrams ; the same is true of the *Corylus* curve in many cases. But the question of whether either of these trees actually spread into areas previously occupied by *Ulmus* is difficult to answer. In the Fallahogy ' clearance phase ' (Smith, 1958 c), probably the most detailed example so far published, the rise of the *Alnus* curve takes place immediately the *Ulmus* and *Pinus* curves fall ; this might be taken as suggesting that the increased *Alnus* percentages are due merely to reduction of the amount of *Ulmus* and *Pinus* pollen reaching the mire surface (and the same might be true of the increased percentages of *Quercus* pollen). On the other hand the rise of the *Corylus* curve takes place at a higher level than the decline of the *Ulmus* and *Pinus* curves ; although it cannot be proved, it seems more likely that this rise of the *Corylus* curve represents an actual invasion, recovery or expansion than is the case with *Alnus*. Had it been that an understory of hazel was enabled to flower by the removal or death of shading trees, then one would have expected a more immediate rise of the *Corylus* curve.

In most of the Irish pollen diagrams the *Ulmus* curve regains its former values soon after the first decline. This behaviour of the *Ulmus* curve may indicate that the elm was able to regenerate, but we should examine the possibility that the resurgence is more apparent than real. It might be argued that the recovery of the *Ulmus* curve is due to the reduction of the values for the other curves, but this would mean the simultaneous death or destruction of a number of all the other trees which, while not impossible, seems unlikely.

At the two sites for which it has been given (Fallahogy and Parkmore), the curve for the ratio between tree pollen and non-tree pollen does not rise markedly during the recovery of the *Ulmus* curve. This apparently indicates that there was no general disforestation at the same time as the ‘ clearance phase ’ ; although, unfortunately, the ratio curve cannot be regarded as a completely reliable indicator of the progress of disforestation since some pollen types that might have come from plants of the mire surface are, perforce, included in the non-tree pollen sum. If there were evidence for a general disforestation, or a continued disforestation after the ‘ clearance phase ’, then we might be justified in saying that the recovery of *Ulmus* is only apparent, or at least that it did not regain its former status.

It does not seem unreasonable to suppose, however, that the elm was able to recover, either by recolonization or by recovery of injured trees (or by a combination of both processes), and that it re-occupied its former habitats. On the other hand, it is impossible to be certain that it regained precisely its former status. Even with this proviso, it can hardly be that the growth of elm was climatically limited during the time of the recovery. There appears to be no need to postulate the beginning of a *maintained* change of climatic conditions at the first *Ulmus* decline in Ireland. As we have seen, however, a short term climatic fluctuation cannot be ruled out.

After the second decline the *Ulmus* curve rarely rises again to its former values, but there is a continued rise and fall of the curve which often tends to reciprocate with the *Plantago lanceolata* curve. The second decline of the *Ulmus* curve is what Mitchell (1956) refers to as the ‘ general ’ decline, and he inclines to the view that after the climatic optimum of the early Post-glacial period conditions turned against *Ulmus* and that its general decline was accelerated by human activity (Mitchell, 1956 : 242). He goes on to say that since the first ‘ Landnam ’ phase in Ireland preceeds the general decline of *Ulmus*, whereas in Denmark it occurs after the general *Ulmus* decline, we might conclude that agriculture reached Ireland before it reached Denmark. We may point out here, though, that in the diagram from Saekkedam, Iversen places the Danish zone boundary VII–VIII at a decline of the *Ulmus* and *Hedera* curves after the ‘ Landnam ’ phase ; a pattern very similar to the pattern of the Irish pollen curves.

Mitchell (1958 : 52), in his paper on radiocarbon dates and pollen zones in Ireland, says that since the *Ulmus* decline in Holland and England has been radio-carbon dated to about 3000 B.C. the same must be true of Ireland. The radio-carbon dates that Watts has given, in this symposium, would appear to

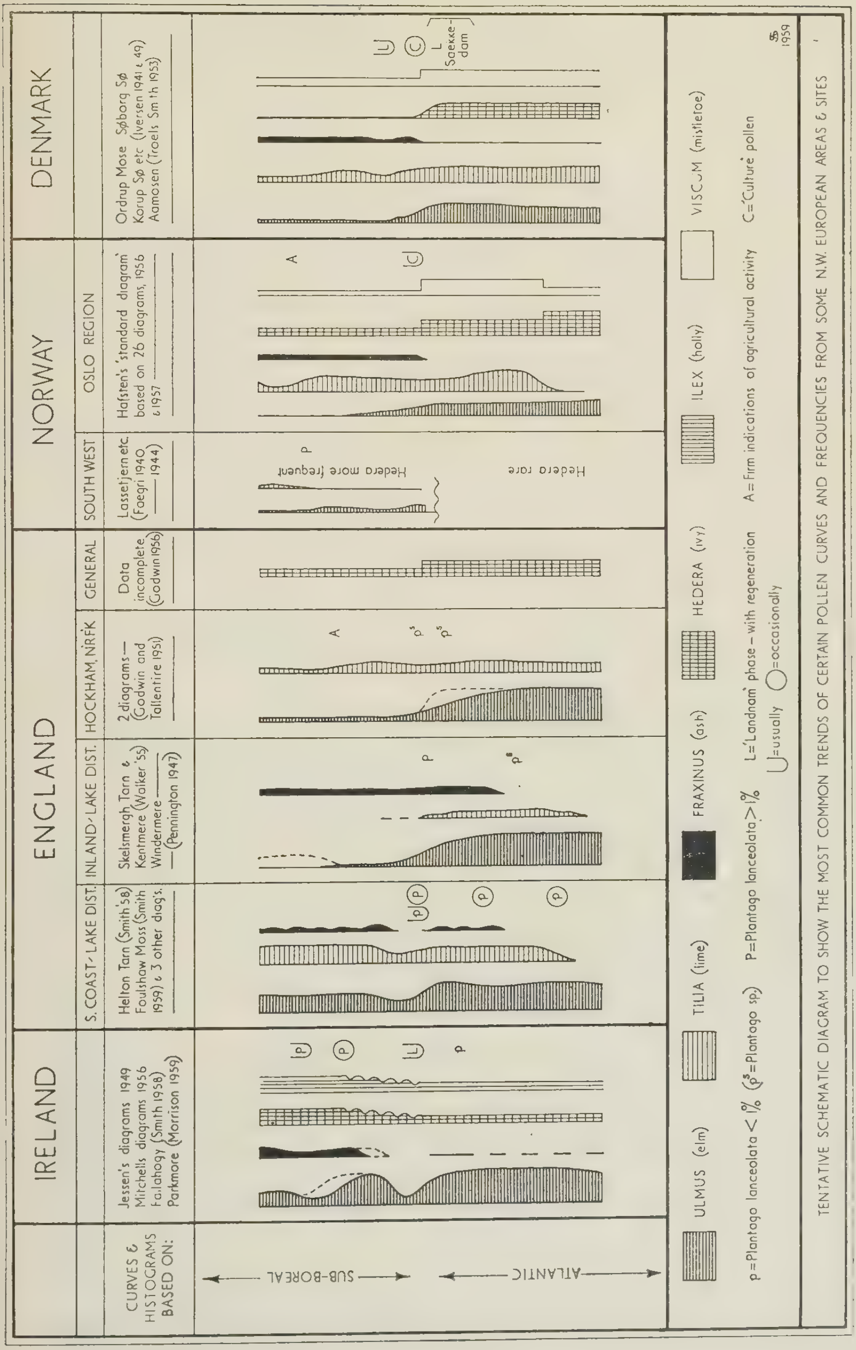
IRELAND
ENGLAND
NORWAY
DENMARK
S. COAST- LAKE DIST.
INLAND- LAKE DIST.
HOCKHAM, N'R'F'K
GENERAL
SOUTH WEST
OSLO REGION
CURVES & HISTOGRAMS BASED ON:
Jessen's diagrams 1949 Mitchells diagrams 1956 Fallahogy (Smith 1958) Parkmore (Morrison 1959)
Helton Tarn (Smith '58) Foulshaw Moss (Smith 1959) & 3 other diag's.
Skelsmergh Tarn & Kentmere (Walker '55) Windermere (Pennington 1947)
2 diagrams (Godwin and Tallentire 1951)
Data incomplete (Godwin 1956)
Lassetjern etc. (Faegri 1940 1944)
Hafsten's 'standard diagram' based on 26 diagrams, 1956 & 1957
Ordrup Mose Søborg Sø Korup Sø etc (Iversen 1941 & 49) Aamosen (Troels Smith 1953)
SUB-BOREAL
ATLANTIC
Hedera more frequent
Hedera rare
Saekkedam
ULMUS (elm)
TILIA (lime)
FRAXINUS (ash)
HEDERA (ivy)
ILEX (holly)
VISCUM (mistletoe)
p=Plantago lanceolata < 1% (p^s=Plantago sp.)
P=Plantago lanceolata > 1%
L='Landnam' phase – with regeneration
U=usually O=occasionally
A=Firm indications of agricultural activity
C='Culture' pollen
TENTATIVE SCHEMATIC DIAGRAM TO SHOW THE MOST COMMON TRENDS OF CERTAIN POLLEN CURVES AND FREQUENCIES FROM SOME N.W. EUROPEAN AREAS & SITES
1959

FIG. 1.—Tentative schematic diagram to show the most common trends of certain pollen curves and frequencies from some North-West European areas and sites. Little attempt has been made to represent the actual values of the pollen curves and histograms. Features drawn at the same level are not necessarily synchronous. *Ilex* has been omitted for England, and *Fraxinus* for South-West Norway. For full explanation see text.

support this preliminary assumption. But it would be wrong to assume, at this stage, that the first decline of *Ulmus* was necessarily synchronous at all Irish sites. At Cannons Lough in mid-eastern Co. Derry, for instance, (Smith, unpublished) the first decline of *Ulmus*, with associated small amounts of *Plantago lanceolata* pollen occurs so soon after the end of the Boreal period that it is difficult to believe that the *Ulmus* decline is as late as 3000 B.C.

A recovery of either the *Ulmus* curve or the *Tilia* curve in the English pollen diagrams is rare, but in the southern part of the Lake District it is apparent that regeneration of lime, and to a certain extent of elm, took place after a temporary decline at the beginning of Sub-boreal time. Five sites have been investigated in the south-western corner of Westmorland, none of which is more than three miles (5 km.) from the coast. Broadly speaking the sites are scattered around the massive Carboniferous limestone block of Whitbarrow (Smith, 1958 b, 1959). In all the diagrams, values for *Tilia* pollen in the Sub-boreal are as high, or higher, than in the Atlantic period. The *Ulmus* values in the Sub-boreal are somewhat lower than in the Atlantic period, but there appears to be a decline of both curves at the zone boundary, followed by a recovery. It must be borne in mind, however, that the diagrams referred to are only a preliminary survey and that some of them are complicated by the presence of *Betula* pollen of local origin. The more detailed work that has been carried out by Oldfield (unpublished) will no doubt amplify the present information.

Some ten miles inland, Walker's diagrams (1955) show a cessation of the *Tilia* curve and a more or less gradual decline of the *Ulmus* curve at the Zone VIIa–VIIb boundary.

It seems likely, then, that if a climatic change were responsible for the general decline of *Tilia* observed at the Atlantic/Sub-boreal transition in northern England, it was of such a character that its effects could be overridden by locally favourable conditions in the southern part of the Lake District. The predominantly south-facing calcareous slopes and the proximity to the sea were no doubt largely responsible for the continued abundance of *Tilia* in this region. On the other hand, to judge from the amount of *Plantago lanceolata* pollen in the Sub-boreal, agricultural activity was not intense, and it might be argued that *Tilia*, and perhaps *Ulmus*, remained relatively abundant for this reason. But in Donner's diagrams from Oban, Argyllshire (Donner, 1957) there is little evidence for human activity in the Sub-boreal period, and yet still a marked decline of *Ulmus*. It must be recognized, however, that absence of evidence is not a strong argument for absence of human activity.

Tilia pollen is virtually absent from Donner's diagrams, and it is difficult to point to a site with a marked, and maintained, decline of the *Tilia* curve where there is no evidence of human activity.

There are, of course, many factors besides changed climatic conditions that might have checked the regeneration of *Ulmus* and *Tilia*. Perhaps the most important possibilities are human activity, changed soil conditions, persistent disease, occupation of the suitable habitats by other species, and lack of seed parents. Some of these factors, however, might have led to only a temporary check of regeneration.

As an example of the possible effects of competition one might point to the behaviour of the *Pinus* curve in Irish pollen diagrams. There is often a decline of the *Pinus* curve at the first *Ulmus* decline, and in many cases in the southern part of the country, the curve does not regain its former values. In the north the *Pinus* curve usually recovers and then falls again at the second decline of *Ulmus*. Where the curve does not rise again, we might suspect that it signifies that pine was not able to compete with other species for its previously occupied habitats. There is no evidence to show that in the Atlantic period in the Irish lowlands pine was growing on soils which were too poor to support other species. It seems likely that pine persisted on the less fertile soils from its widespread Boreal distribution. In support of this hypothesis one might draw attention to the slow decline of the *Pinus* curve and gradual rise of the *Quercus* curve in the Atlantic period. This pattern might well indicate the slow replacement of pine by oak. It may be that once pine was removed by some agency from soils of intermediate fertility it was not able to return owing to its low competitive power.

As far as soil conditions are concerned, it appears that even in Ireland where regeneration of elm has apparently been common after the first decline, the regeneration may well have been limited to some extent by poor soil conditions. Cannon's Lough, Co. Derry, is in a local area of sandy eskers, and only three miles (5 km.) away from Fallahogy where the recovery of elm is conspicuous. Fallahogy lies in an area of boulder clays. At Cannon's Lough the elm curve does not regain its former level, the decline and recovery are slow, and the intervening period, with abundant *Plantago lanceolata* and cereal pollen, is prolonged. A permanent alteration in the local vegetation after the *Plantago* maximum is probably indicated by the sustained higher levels for Gramineae, Cyperaceae, and Ericaceae. It seems likely that abandoned fields and pastures were never fully recolonized by woodland. It is difficult in this case to escape the conclusion that the poor soil conditions, while aggravated by human activity, were primarily responsible for the non-recovery of the vegetation.

Evidence from these two sites, and from others in close proximity, seems more and more to indicate that in the Post-glacial period many pollen diagrams reflect rather local vegetation changes. Further investigation of closely spaced sites in critical areas will no doubt continue to increase our understanding of what Faegri and Iversen (1950) have termed the palaeophysiognomy of the vegetation.

To sum up, it might be said that at the transition between the Atlantic and Sub-boreal periods a case can be made for the action of one or more of the following factors in different areas : climatic change, the activities of man (and his domesticated animals), disease, edaphic conditions and ecological competition. Clearly the effects of these factors would have been dependent on the pre-existing conditions. In different geographic and topographic regions the conditions must always have varied, and it may well be that in diverse regions different factors have been of critical importance. There appears to be no incontravertible evidence that any one factor was of over-riding and universal importance. There is little doubt, however, that, in closely circumscribed regions there will be a continued attempt to delimit the causes of the vegetational changes insofar as these changes can be determined from the type of evidence available.

The most reasonable broad view, at the moment, appears to be that climatic change, human activity and perhaps disease have been primarily responsible for the vegetational changes at the Atlantic/Sub-boreal transition ; but that the importance of these factors may well have varied from region to region, and doubtless their effects have been modified by the more local factors of soil conditions and ecological competition.

ADDENDUM

Since this paper was written two important contributions to the topic have appeared. Troels Smith (1960) has given further strong arguments in favour of his view that, in Denmark, the vegetational changes at the Atlantic/Sub-boreal transition most probably register the introduction of a form of agriculture based on stalled cattle fed on leaves of elm, ash and other plants. While accepting this view, with some reservations, Iversen (1960) has sustained his argument that the decline of *Hedera* in the Sub-boreal is a reflection, at least in part, of a climatic change. Further, Iversen has amplified his earlier views on the nature of the climatic conditions in the period under review.

These two contributions serve to emphasize the need, at the moment, for taking the broad view set out at the end of the present paper, and the value of looking for explanations in terms of several interacting physical and biological factors.

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5. THE FULL- AND LATE-GLACIAL PERIOD IN SOUTH-WEST FRANCE

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IN 1957, I was given the opportunity of investigating the Quaternary sites in the neighbourhood of Biarritz. Mostly they comprised cliff-exposures containing rich and varied organic deposits which, from their stratigraphical contexts appeared to be mainly Interglacial or Interstadial in character. None was demonstrably Late- or Post-glacial. It was felt that in order to be able to ascertain the Interglacial nature or otherwise of these deposits, on the basis of the most usual climatic criterion[1], and in order to be able to distinguish them from the local Post-glacial succession, the first task was the discovery and investigation of an undoubted Post-glacial site. Accordingly, one was chosen not three miles from most of the coastal exposures referred to above, an inland basin in which the apparently recently dried out surface, the lack of any degree of compaction and the almost complete absence of superuncumbent strata pointed to a Post-glacial date. This was confirmed by the presence, in the upper levels of the pollen series, of various introduced species, of indications of deforestation and human activity and of cereal-type pollen.

The bottom two and a half metres of the pollen series, taken from the central and deepest part of the basin, showed characteristics which, by analogy with Northern Europe, marked the presence of a probable Late-glacial succession. Notably there was : –

(a) an almost complete absence of deciduous thermophilous forest trees ;
(b) high frequencies of non-tree pollen-types relative to tree pollen-types ;

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[1] That the climatic indications of the vegetation present at the climatic optimum of an Interglacial period should be not less favourable than those indicated by the flora and vegetation at the Post-glacial climatic optimum in the same area.

(c) the presence of species and genera not growing in the area at the present day and either restricted to, or more characteristic of areas of severe climatic conditions ;

(d) the presence, within the series, no matter what total the calculations were based on, of changes in pollen frequency of an oscillatory nature.

What follows is an exposition and interpretation of the lower part of this single pollen series. It is acknowledged that some of the conclusions reached from a consideration of this single diagram badly need confirming from other nearby sites.

Despite a good deal of stratigraphical work at the site, the relatively simple correlation between pollen-analytical changes and stratigraphic sequence which so often emerges from a comparable investigation in Britain was not discovered. The explanation is thought to lie in the nature of the circumperipheral deposits and in the conditions under which the sediments of the basin were laid down.

The first consideration in the interpretation of the diagram seemed to be the choice of criteria, within the pollen-analytical succession, which would reflect the vegetational changes on the surrounding dry land during the period represented, and thus form the basis of a subdivision of the diagram, perhaps a zonation scheme which would allow the series to be correlated with the established North-West European succession. Many undoubted aquatic types are strongly represented in the diagram. Not only could they be excluded from consideration as dry-land vegetation indicators, but their changes in relative frequency allowed some postulation as to the nature of local hydroseral developments at certain stages in the series. Also, throughout the diagram, many herbaceous ' heliophilous[2] ' taxa are represented and these could be taken to indicate the extent of open insolated habitats. The pollen types in this category were carefully selected after reference to all the available French Floras. However, at many levels, the representation of pollen types whose climatic and ecological significance was not clear preponderated, e.g., *Gramineae*, *Cyperaceae*, *Empetrum nigrum* L. sens strict., *Calluna vulgaris* L., etc.

The changes in frequency, in the diagram, of these latter less illuminating types has been compared with that of both the heliophilous species and of the aquatic species. They fell into three categories :

(i) Those whose variations seemed, at least at some point in the series, to be related to some element in the aquatic succession. In each case, the ecological role of these types, as deduced in this way from their correlation with the aquatic succession, was compatible with the ecological relationships of some aquatic or semi-aquatic member or members of the group—e.g., the correlation between the curve for *Gramineae* and that for *Typha* and *Sparganium* type could be understood in terms of the presence within the *Gramineae* of such reedswamp species as *Phragmites communis*, Trin. In this instance, macroscopic remains of *Phragmites* confirmed the deduced correlation. Such pollen types which, at least in some part of the series could be related to probable hydroseral developments were assumed, in part at least, to represent aquatic or semi-aquatic taxa, and thus their variations were not considered in trying to determine the dry-land succession.

(ii) There were those whose frequencies could be related, in the same way, to the changes in frequency of some at least of the herbaceous heliophilous flora present. The presence of commonly heliophilous genera and species within these taxa, (e.g. *Liguliflorae*) made the correlation quite plausible in most cases.

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[2] This word is used throughout in the negative sense merely to denote dry-land species and genera the individuals of which might not be expected to thrive under forest cover and the relative frequencies of which might be expected to furnish some indication of the extent of unforested land in the neighbourhood.

(iii) There were, in addition, still many types, the ecological significance of which could not be determined in this way. The *Empetrum* and *Calluna* pollen found fell into this category. The enormous and interrelated frequencies of both could not be attributed certainly either to local topogenous hydroseral development or to circumperipheral heath formation.

As a result of this analysis, pollen types were selected comprising definite herbaceous heliophilous taxa, and also taxa including heliophilous species and genera, the representation of which seemed to be related to the changing frequencies of the definite heliophytes. The representation of the definite heliophytes has been recorded and plotted as a percentage of both the tree pollen sum and also as a percentage of the total non-aquatic pollen sum including trees, shrubs and herbs.

This allows the subdivision of the period of time represented by the diagram into supposedly relatively more or less forested episodes. Since the conditions at the base of the diagram represent undoubtedly a treeless landscape, and since there is no direct evidence, as yet, to suggest that in the last glacial period there was anything other than this type of landscape between the extended polar and northern montane ice-caps on the one hand, and the Pyrenean valley glacier snouts on the other, then one cannot assume the presence, in western Europe at this time, of any geographical or ecological barriers between the northern and southern ice-margins in question. Thus it is not possible to be sure, initially, to what extent the glacial flora in the south-west of France was derived from northern or Pyrenean sources, nor can one say whether the glacial vegetation bore a closer relationship to present day northern or present day high-pyrenean plant communities, since, from the area, retreat of the glacial flora both to the north and uphill into the Pyrenees could, in theory, have taken place in Post-glacial times. However, both near the Pyrenean altitudinal and the polar latitudinal limits of vegetation the degree of forest cover is an indication of climatic severity in most cases, and so there is some justification in the first place, in using it here as an index of the climatically induced dry-land vegetation changes.

The zonation scheme does not rest solely on this index derived from the tree/heliophyte ratio. Except for the bottom 50 cm. of the series, where there is no definite evidence for the presence of tree species in the neighbourhood, the relationship between the curves for *Pinus* and *Betula*, the only two Late-glacial tree pollen types consistently represented, is synchronous with the variations in the heliophyte curve. Pine predominates along with the peaks of heliophyte representation, birch in the less heliophilous intervals. The birch found was all definitely tree-birch. Most of the pine pollen recorded from these levels differed from typical *Pinus silvestris* L. pollen in having a smaller body size in relation to the air-sacs, a slightly smaller absolute body size and a slightly different emplacement of the air sacs. It was very closely comparable with pollen of the *Pinus montana* Mill. type, of which the Pyrenean species is often referred to as *Pinus uncinata* Ram. The absence of dwarf birch in the Pyrenees and its presence in Northern Europe, and the presence of *Pinus uncinata* in the Pyrenees and its absence in Northern Europe would tend preliminarily to link the glacial flora represented here with the present high Pyrenean vegetation rather than the circum-arctic. A small point supporting this is the presence of *Taxus baccata* L. pollen in significant quantities at one point in this lower part of the diagram. *Taxus* in France, especially in the Alps and Pyrenees, is above all a sub-montane species ascending even today to some 5500 ft.

Working on the basis of this analogy with the Pyrenees, the relationship between the pine/birch ratio and the tree/heliophyte ratio is easily explained.

Pinus uncinata ascends to greater heights in the Pyrenees than any other tree species and forms the tree-line almost everywhere. Birch is a lower element. Thus the linking of the high pine and high heliophyte, and the high birch and low heliophyte percentages is in accordance with the present day affinities of the flora represented. It seems likely that both ratios are reflecting consistently degrees of climatic severity.

From these two lines of complementary evidence a succession of vegetational changes can be deduced which, bearing in mind the most likely causative climatic changes underlying the vegetational sequence, can be correlated, with perhaps dangerous plausibility, with the usually accepted West-European sequence.

The first zone has been labelled Zone F, and is taken to represent the end of the Full-glacial period in the area. In this zone, trees never exceed 3 per cent of the total non-aquatic pollen rain. They comprise pine and the thermophilous types such as *Quercus* sp., *Fagus* sp. and a little *Corylus*. From the absence of *Betula* from the pollen rain at this level and from the very low frequency and in one case total absence of pine too, it is considered improbable that these other, more warmth demanding trees existed in the area at the time. Indeed, such a low representation of *Pinus* suggests that it, like birch, was absent too. The presence of the other trees was not demonstrably a consequence of derivation—the quality of preservation was perfect—and so it is possible that they are a result of long distance transport, although the danger of contamination from higher levels during boring also exists. No great floral richness is suggested by the evidence from this level. Only 19 pollen types are represented as compared with 51 in the next zone. This may be partly a reflection of the fact that 3 times as many grains were counted in the next zone though over 900 were counted in Zone F. Along with the absence of trees one notices the absence of aquatic species and also of the more ‘ steppic ’ species and genera of the later zones. In particular, the pollen type identified here as *Polygonum viviparum* L. was abundant. *Cryptogramma crispa* (L.) Hook & Bauer, which is recorded as not descending below 3000 feet at the present day in the Pyrenees was present. Severely cold, but not demonstrably dry conditions appear to be recorded.

The next zone I have called L.1. It sees the first occurrence of most of the shrub pollen-types, the *Ericales*, birch and yew and the aquatics, as well as those heliophilous taxa with steppe affinities, e.g. *Artemisia* sp., *Centaurea* sp., *Centaurea cyanus* L., *Ephedra distachya* L. The F/L.1 transition is a very clear horizon and it is here used to define the beginning of the local Late-glacial. If the occurrence of the steppe element at this level records an increase in continentality and summer warmth, then perhaps this would account for the incoming trees and shrubs without necessarily any overall rise in average annual temperature having occurred. The area still seems to have been mostly open and unforested.

The next horizon records a great decrease in the heliophilous representation and an increase in the tree pollen, especially birch, preceded by a rapid ephemeral increase in an unknown species of willow. The concurrence of these two facts at this level suggests the presence of a warm period, which has been called Zone L.2. The frequency of the heliophytes is greatly reduced, and the absence of the steppe genera at this level, the high frequencies of birch and willow, and the abundance of aquatic types do not mark this period out as a dry one locally. The aquatic succession suggests a rapid rise in the water level at the beginning of this zone. It is thought to be contemporary with some at least of the pre-Allerød warm phases defined elsewhere in northern Europe.

Zone L.3 marks the return to more open conditions, the frequencies of both pine and the steppe plants increasing. Open scattered *Pinus uncinata* communities can be observed near the tree-line in the Pyrenees at the present day. A return to colder and perhaps drier conditions seems to have been recorded. The *Ephedra* from this zone and the *Hippophaë Rhamnoides* L. would both be very much in context on the uniformly sandy slopes surrounding the site. The end of this zone sees the temporary spread of *Empetrum nigrum* L. sens. strict., accompanied by some *Calluna*. This could represent a colonization of the herb-dominated landscape by heath communities. Equally, it could be the ' end-product ' of the local aquatic succession which can be traced in the diagram—i.e. open water, succeeded by reedswamp, followed by *Sphagnum*. This zone can be correlated with the last pre-Allerød climatic deterioration and glacial advance in Northern Europe in all likelihood, and would thus be the equivalent of the top of British Zone I.

Zone L.4 sees the first period of probable birch dominance, initially with *Salix* and *Pinus* as previously. The forest evidence for ameliorating climate is much stronger than in Zone L.2, and this phase I correlate tentatively with the Allerod period, (British Zone II).

Zone L.5 records a slight revertance to more open conditions with pine predominating in the tree pollen diagram and the herbs increasing simultaneously. This, the last phase of climatic deterioration recorded here before the opening of the Post-glacial period, is probably the equivalent of British Zone III. The zone ends with the rational boundary for *Quercus*, the first deciduous thermophilous forest tree to be significantly represented in the diagram, which is taken to indicate the opening of the Post-glacial period. Birch increases temporarily at this point, until the oak maximum is reached, further confirmation of the supposed role of birch as a sub-montane element in the vegetational development.

The sequence described above can be paralleled in Norther Europe by evidence from those sites where a Pre-Allerød warm period has been detected, separated from the Allerød by a distinct cold interval.

The possible main palaeo-ecological and biogeographic conclusions of the present study can be summarized as follows :

(i) It seems likely that this part of South-western France could not have formed a per-glacial refugium for most of our thermophilous North European species.
(ii) The most consistent and cogent interpretation of the Full- and Late-glacial vegetational sequence represented can be related to that found in the more complete diagrams from Northern Europe.
(iii) The Full- and Late-glacial flora and vegetation of the area probably bore a closer relationship to the present day high-Pyrenean plant communities than to those of the present day northern circum-polar tundra.
(iv) The presence of a steppe-element in the Late-glacial flora at certain times is demonstrated.

6. POST-GLACIAL HISTORY OF JUNIPER IN SCOTLAND

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Although *Juniperus communis* is still a widespread species in Scotland today there is evidence that its range has been considerably reduced within recent times. Scattered plants are found throughout the country and Fig. 1 shows the present distribution of vegetation in which juniper is one of the principal constituents. The solid line encloses occurrences of tall juniper scrub, either as an understory to pine or birch or as a non-woodland community within, or just above, the present potential forest limit. These scrubs are formed by ssp. *communis.* The broken line indicates the extent of dwarf, but not prostrate, juniper scrub, either well above the present forest limit or at sea leavel on the coast. This form agrees well with ssp. *nana* or *montana* as understood in Scandinavia. Crosses indicate the occurrence of tall or dwarf juniper scrub on small islands in freshwater lochs outside the range of the ' mainland ' distribution.

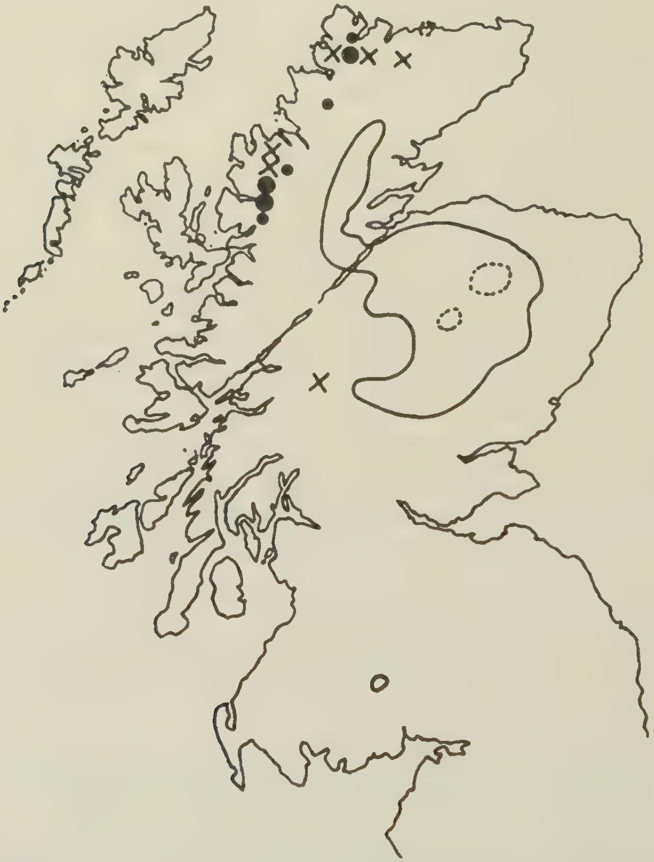

FIG. 1.—Distribution of vegetation types in Scotland, in which juniper is a principal constituent : for details see text.

The black dots show the distribution of prostrate juniper scrub as described by Poore and McVean (1957). The smaller dots mark fragmentary stands only. This form of juniper, commonly referred to as ssp. *nana* in Britain may have the leaf characters of ssp. *communis* and the taxonomic position is somewhat confused.

British Post-glacial juniper records to date have been collected and published by Godwin (1956) and the situation can be summarized as follows. Palynologists can now recognize the pollen of juniper at the generic level and considerable frequencies have now been recorded from the Late-glacial/Post-glacial transition in north-west England and southern Scotland. Remains of leaves, stems, fruits and seeds have been found once in Full-glacial and several times in Zones II and III of Late-glacial times. In the Post-glacial, *Juniperus* has been identified in Zones V, VI, VI–VII and VIII so that it seems probable that it formed an important part of the Late-glacial vegetation and that it has persisted in this country right through from Full-glacial times. In Scotland the record is meagre. Dr. Godwin has recorded the pollen from Zones III–IV in Whitrig Bog, Berwickshire, but there appear to be no records of macro-fossils even in Lewis (1905–1911).

A recent study by Durno and McVean (1959) attempts to relate the present vegetation of the Beinn Eighe Nature Reserve in Ross-shire to what can be discovered of the Post-glacial history of the area by pollen analysis and an examination of the peat stratigraphy. They record prostrate juniper stems from peat of Zone VIIb (Sub-boreal) at 1900 ft, within one mile of living prostrate scrub and conclude that the community is therefore of some antiquity. The Sub-boreal scrub appears to have been overwhelmed by rapid bog growth but in view of the important role of forest and scrub fires demonstrated by Durno and McVean in this area it seems quite likely that fire was involved in such a change in vegetation. Unidentified fragments of charcoal from the base of this profile (lower zone VIIa) may also be of juniper but it is not certain whether the abundant dead stems that can be found scattered over the ground in the Cambrian quartzite and Torridon sandstone regions of north-west Scotland have been derived from eroded peat or represent the remains of more recent scrub which has been destroyed by moor fires.

Sub-fossil juniper stems can readily be identified by the characteristic scent of the wood and by using this method I have made a rapid survey of juniper remains in peat over the last few years. Stems of the same form as those occurring in living prostrate scrub are widespread in blanket peat deposits from about 1200 ft to 2000 ft throughout the north-west Highlands. At lower elevations (500 ft to 1000 ft) juniper wood is more sparsely distributed and mingled with the remains of pine and birch, the stems having an upright rather than a prostrate form.

In the central Highlands juniper remains have been found in the peat up to an altitude of nearly 3000 ft at Loch nan Stuirteag in the Cairngorms but none of the stems have approached the extreme prostrate form of the north-west.

It has not been possible to date any of these levels but it seems reasonably certain that they are of the same age as the principal horizons of pine remains with which they are frequently connected.

There is thus some evidence that the present distribution of juniper communities represents the fragmentation of a more continuous post-glacial cover and that juniper scrub was once an important element of the vegetation at the upper forest limit. Fire appears to have been the principal factor responsible for the reduction, particularly in the north and west where juniper is now confined to islands, inaccessible ledges, and one or two north facing slopes which provide a rather peculiar habitat. It also seems likely that the various growth habits of juniper, from the tall upright tree forms of the forest zone to the extreme prostrate shrubs of higher levels, have existed since Atlantic times at least and that they were once connected by a continuous series of intermediate types. Deforestation and fires have broken the continuity and resulted in apparently distinct varieties or sub-species.

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7. SOME CLIMATIC AND EDAPHIC INDICATIONS FROM THE LATE-GLACIAL FLORA

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Most of the Late-glacial species discussed here came from Whitrig Bog in southern Scotland. This site lies to the east of the Moffat Hills and to the south of the Lammermuirs, about three miles north of the Tweed and at 435 ft o.d. (133 m.). It is within the area of the Scottish Readvance, but outside the Lammermuir-Stranraer moraines (Donner, 1957).

The deposits showed a typical Late-glacial sequence of an organic mud and marl lying between lower and upper silty clays. The three layers are correlated with Zone II, and Zones I and III respectively. Below the Zone I clay lay boulder clay, presumably related to the Scottish Readvance ; and Post-glacial marl and peat overlayed the Zone III clay. Pollen-analysis by Dr Godwin accords with this stratigraphic zoning.

The determinations, with one or two exceptions, are based on macroscopic material, seeds, fruits, leaves etc. Only the terrestrial species from Zones II and III will be referred to.

From the Zone II muds and marl the occurrence of tree-birch fruits supports the indication of Park Tundra deduced from the greater abundance of tree and shrub pollen relative to that in the zones above and below ; and *Filipendula ulmaria*, although a marshplant, suggests ' warmer ' conditions.

In Zone III many of the species (Table I) are of ' arctic-montane ' affinity. Many were concentrated in a marked leafy layer near the base of the silty-clay, where large quantities of the leaves, fruits and buds of *Salix herbacea* were present.

Table I.—Macroscopic remains of land plants from Zone III at Whitrig

Armeria maritima (Mill.) Willd.
Betula nana L.
Draba incana L.*
Empetrum nigrum agg.
Luzula spicata (L.) DC.
Oxyria digyna (L.) Hill
Papaver sect. *scapiflora*
Polygonum viviparum L.*
Rumex acetosella L.
Salix herbacea L.
Salix reticulata L.*
Saxifraga hypnoides L.*
Saxifraga cf. *rivularis** or *cernua*
Saxifraga cf. *rosacea*
(*Selaginella selaginoides* (L.) Link.)
Thalictrum alpinum L.*

Pollen : *Koenigia islandica* L., *Ephedra distachya* L.

* Basophilous species.

These, and other Late-glacial species will be discussed for their value as indicators of climatic and edaphic conditions. The indications of maximum summer temperature will be considered in some detail. But before conclusions can be drawn from this or any other list of determinations certain precautions are necessary.

The adequacy of the taxonomic determination is the basis upon which ecological deduction rests. Thus type material must represent the full range of morphological variability and geographical source ; and full cognisance must be taken of taxonomic situations which might else give misleading determinations. Closely allied species, or sub-species or polyploid races within an aggregate may each have different ranges and requirements so that the validity of deductions made from the present-day range will depend on the taxon represented. An example from Whitrig, Zone III, is *Papaver* sect. *scapiflora* (Conolly, 1958).

Certain aspects of the climate of Late-glacial times are sometimes deduced from the past and present distribution of records for a single species, but this is of limited value without detailed autecological knowledge.

The assemblage of species from a site can be tabulated to show the proportion of categories having different geographical limits. Northern limits for the more southerly element, and southerly limits (of continuous distribution) for the more northerly species are indicative but can only lead to conclusions about climate in general, and not to one particular component.

A more precise criterion of climate has been proposed by Dahl (1951) who suggested that the distribution in Scandinavia of many of the mountain species is correlated with mean annual maximum summer temperature. Observations on the behaviour of certain mountain plants in cultivation in lowland Norway suggested that high summer temperatures were deleterious, even when the plants were adequately watered. Many of these same species descend nearly or quite to sea-level on parts of the Norwegian coast, especially the more climatically ‘ oceanic ’ parts.

Dahl prepared two isotherm maps to show estimated mean annual maximum summer temperature, one map of values reduced to sea level and a second of deduced actual values for the highest mountain tops. These summits are presumed to be the coolest places in a given area and thus are most likely to provide suitable localities for species limited by high summer temperatures. The sea level isotherms revealed that the areas where the arctic-montane species descended to sea level were just those places where the lowest coastal values occur. Using the second isotherm map he found that the distribution limits for a considerable number of the mountain species coincided (for all but a few stations) with particular isotherms : i.e. the limit of *Sedum rosea* corresponded with the isotherm for 25° C., that for *Salix herbacea* with 26° C., *Dryas octopetala* with 27° C., and *Koenigia islandica* with the isotherm for 24°C. Dahl concluded (*op. cit.*, p. 42) that a close correlation exists between the maximum summer temperatures and the cause or causes delimiting the distribution of these plants. It should be noted that the actual temperatures experienced by the plant depend on the microclimate, but ‘ the probability that there will be localities with a (suitable) microclimate . . . is correlated with macroclimate ’ (*op. cit.*, p. 31)—hence the correlations between macroclimate and distribution obtained.

Finally Dahl pointed out that although Late-glacial finds of *Salix herbacea* are common in Denmark and in Skåne (S. Sweden) there are no records from sites in Central Sweden : this, he suggests, is because, although temperatures were favourably low in the early part of the Late-glacial (Zone I), during the ensuing Allerød period (when the ice margin retreated from Skåne to Central Sweden) it rapidly became too warm for *Salix herbacea* although it survived in Denmark. On the other hand species like *Dryas octopetala*, whose limiting isotherm is 27° C. (i.e. higher than that for *S. herbacea*) were not eliminated during the Allerød warm period, and these species are in fact found in Late-glacial sites of Central Sweden.

It seemed possible that similar correlations held for the British Isles and a few have been investigated.

Firstly, many mountain species in this country, as in Norway, reach low altitudes on coasts, especially in West Ireland, N.W. Scotland and the Shetlands (Table II). And many of the Late-glacial species from Whitrig or other sites are among them, for example *Salix herbacea, Sedum* cf. *rosea*[1], *Thalictrum alpinum, Polygonum viviparum.*

Isotherm maps similar to the two Scandinavian ones described above have been prepared for the British Isles using data provided by Dahl. And in certain coastal areas a similar correspondence between *low* sea-level isotherms calculated as above and the occurrence of considerable numbers of mountain species is shown. For example the sea-level isotherm for 24° C. clearly delimits many of these areas such as the extreme west coast of Ireland (Kerry, Achill Is., Mayo, Donegal), the Outer Hebrides, the North-west Highlands in the Cape Wrath area and in S.E. Caithness, and the Shetlands.

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[1] A pollen-grain of a *Sedum* tentatively assigned to this species from Mapastown, Co. Louth, Zone III (Mitchell, 1953).

TABLE II.—Arctic-alpine species descending to sea-level or low levels

	Ireland West Coast	Scotland N.W.	Shetlands	Faeröes	Iceland
	(ft)		(ft)		(ft)
Alchemilla alpina L.	...	...	...	s.l.	...
Arctostaphyllos uva-ursi (L.) Spreng.	s.l.	cliff-tops	200	...	...
Arctous alpinus (L.) Nied.	...	cliff-tops	200	...	...
Cardaminopsis petraea (L.) Hiit.	800	...	50	...	100
Carex bigelowii Torr. ex Schwein.	Not at s.l.	lochs at *c.* 100 ft	<200	...	...
Carex capillaris L.	...	cliff-tops	...	...	...
DRABA INCANA L.	s.l.	Nr. s.l.†	s.l.	s.l.	...
Dryas octopetala L.	s.l.	...	...	...	s.l.
EMPETRUM NIGRUM (agg.)	s.l.	...	...	...	...
Epilobium alsinifolium Vill.	700	...	...	s.l.	...
Epil. anagallidifolium Lam.	...	...	...	s.l.	...
Juncus triglumis L.	...	...	200	s.l.	100
Juniperus communis ssp. *nana* Syme	...	sea-cliffs	...	...	...
KOENIGIA ISLANDICA L.	...	...	...	s.l.	100
LUZULA SPICATA (L.) DC.	...	...	...	s.l.	100
Lycopodium alpinum L.	Not at s.l.	...	...	s.l.	...
OXYRIA DIGYNA (L.) Hill	*c.* 500	sea-cliffs	s.l.	s.l.	100
POLYGONUM VIVIPARUM L.	*c.* 500	sea-cliff tops*	...	...	100
SALIX HERBACEA L.	870	Nr. sea-level on cliffs	*c.* 400	s.l.	100
Saxifraga aizoides L.	s.l.	coast cliff	...	...	...
Sax. nivalis L.	Not at s.l.	...	...	s.l.	Not at s.l.
Sax. stellaris L.	*c.* 500	...	...	s.l.	...
Sax. oppositifolia L.	s.l.	sea-cliffs*	...	s.l.	s.l.
Sedum rosea (L.) Scop.	...	sea-cliffs*	s.l.	...	...
Silene acaulis (L.) Jacq.	*c.* 500	sea-cliffs*	50	s.l.	s.l.
THALICTRUM ALPINUM L.	900	Nr. sea-level on cliffs	<100	s.l.	100
Tofieldia pusilla (Michx.) Pers.	...	s.l.	...	...	100

Species occurring in Whitrig Zone III in capitals.
s.l. = sea-level.
* Also in Outer Hebrides at or near s.l.
† Also in S.E. Caithness at s.l.

The second type of isotherm map was then superimposed on distribution maps for certain mountain species and it was found that the isotherms which delimit the greatest number of localities are in fact 2–3° C. lower than the corresponding ones in Scandinavia. Whereas *Sedum rosea*, for example, in

Scandinavia showed according to Dahl (1951) a correlation with the isotherm for 25° C., it seems that its limitation in the British Isles corresponds more nearly with 24° C. Likewise for *Salix herbacea* Dahl showed a striking agreement between the isotherm for 26° C. and the limits of this species in Scandinavia ; but for the British Isles this is too high and 23° C. gives a closer agreement for Scotland and Ireland, although 25° C. is better for England. These isotherms leave very few outlying stations, and almost none that do not occur on isolated peaks with exceptionally low values.

A minor correction should be made to the figures because the lapse rate used in the calculations (0·6° C./100 m.) is now known to be too low for both countries : both rates should be somewhat higher (0·7° C./100 m. for summer in Norway (Dahl, in lit.), 0·68° C./100 m. for the British Isles (Manley, 1952)). This would require all the figures to be lowered by a very small amount ; and, as the correction needs to be greater for Norway than for this country, a slight convergence of the two sets of figures therefore ensues. However this is not nearly sufficient to account for the difference between the two countries. Again it has been suggested that a lower lapse rate is to be expected in oceanic climates compared with more continental ones. This would argue towards raising the figures somewhat in the more extreme oceanic regions, hence lessening the discrepancies slightly, including that between England and the rest of the British Isles.

If the correlation with a lower maximum summer temperature in the British Isles than in Scandinavia is a genuine one, a possible explanation might be sought in the higher humidity of this more oceanic country. For the plant, which depends for reduction of temperature by loss of heat in transpiration, the humidity of the air is of importance when high temperatures are significant.

If, on the other hand, the correlation with a lower isotherm is a spurious one then other arguments must be put forward to account for the difference. Firstly, common species with large and aggressive populations will by virtue of their ' inoculum ' potential be able rapidly to retrieve marginal or intermediate territory lost during a temporary adverse phase, such as hot summers. On the other hand, rare species with narrow ecological amplitudes and small isolated populations will lack this dispersive ability and hence will be less likely to occupy all the habitats which they are capable of exploiting. They will in fact be under-dispersed. Thus it is to be expected that in regions where a species is under-dispersed it will be limited by a lower maximum summer isotherm. Hence the closer agreement observed with *Sedum rosea*, a more widespread and well-dispersed species, than with *Salix herbacea*.

This effect is enhanced where there are many isolated summits rather than a continuous mountain chain. It would apply with much greater force in the British Isles than in Scandinavia : slight shifts in climate are likely to cause extinctions rather than reductions in area in the former country.

The Post-glacial climatic optimum thus, in this country, probably caused the extinction of rarer species on many of the isolated summits which are theoretically available today. The present distribution of species may more nearly reflect the isotherms of the post-glacial optimum than those of today. If we assume a 2–3° C. rise in temperature for this period then the British isotherm maps will show a remarkably good agreement, i.e. with those obtained by Dahl. Any increased continentality at this time would accentuate the effect.

In the more extreme oceanic regions maximum summer temperature may be replaced as a limiting factor by other components of oceanicity such as excessive dampness and high winds. A single factor is not necessarily limiting throughout the range of a species and some modification is not unlikely. One must accept a multi-factorial basis for the concept of oceanicity and continentality.

Finally, the position of Late-glacial finds has been entered on the maps to see whether they correlate with differing reactions of the species to maximum summer temperature. As yet too few records are available, except perhaps for *Salix herbacea*. For this species there is (so far) an absence of Late-glacial records from S.E. England and E. Anglia: that is those regions with the highest present-day isotherm (30° C. or over); the nearest is that from Aby, Lincs. which lies on the present 28° C. isotherm; all records from this south-easterly region are of Full-glacial or of Inter-glacial age. The most exacting species on the Whitrig list is *Koenigia*, for which Dahl (*op. cit.*, p. 34) suggests a correlation with 24° C. (perhaps equivalent to 21–22° C. in Scotland). Whitrig, the only published Late-glacial locality, lies near the present 26° C. isotherm. But little can be deduced from a single find.

Of the other species for which isotherm correlations have been made, *Oxyria digyna* is almost identical with *Salix herbacea*: in Scandinavia it is correlated with 26° C. and in the British Isles its limit is marked by the 23° C. isotherm and for England by 25° C. Again there are no Late-glacial occurrences in S.E. England nor E. Anglia but only Full-glacial ones. The limits for *Thalictrum alpinum* are the 27° C. isotherm in Scandinavia, but for this country that for 23° C., with 25° C. for England. There are Late-glacial records of *Thalictrum alpinum*, and also *Dryas octopetala*, from S.E. England, which agrees with a correlation with a higher isotherm, as found by Dahl. The present distribution of *Dryas* in England is so restricted and further complicated by its requirements for base-rich soils that no conclusions can be drawn. *Salix reticulata* is also far too rare, although all stations occur within the isotherm for 21° C. (cf. Scandinavian 26° C.).

These latter species suggest edaphic rather than climatic indications. In the Late-glacial flora, *Dryas*, *Salix reticulata*, and particularly *Draba incana* (for which Dahl gave no temperature correlation), together with other species, such as those marked on the Whitrig list (Table I) as well as mosses like *Distichium capillaceum* and *Camptothecium nitens*, all suggest a more base-rich habitat than occurs today at Whitrig or at many of the Late-glacial sites. At Whitrig in addition to the probable abundance of fresh ' drift ' a nearby outcrop of basaltic rock may have provided some calcium-rich soils. The preponderance and wide distribution of ' calcareous ' species in the Late-glacial is well known, but perhaps it would be wiser to use the term ' basophilous ' which has a wider connotation.

The present day restriction of ' rich ' mountain floras in the British Isles to outcrops of ' calcareous ' rocks (used in rather a wide sense) has been emphasized by Ferreira (1959). And Ratcliffe (1959), discussing the Moffat mountain plants, where a (late-glacial) ' relict ' flora still survives in the more sheltered craggy ravines with outcrops of ' calcareous ' rock, points to the absence of these species from otherwise suitable mountains in the vicinity where either cragginess *or* calcareousness occurs alone. There is an implication here that *open habitat* and *freedom from grazing* are requirements for the survival of these species, many of which occurred at Whitrig. Freedom from grazing is probably an important factor also when comparing Post-glacial extinctions and reductions in area in Norwegian and British conditions. The part open habitat plays in the survival of montane species has been dealt with by Pigott & Walters (1954).

Generalized ecological deductions as to the communities represented in Late-glacial times can sometimes be made from the presence of particular species. Certain species from Zone III at Whitrig such as *Salix herbacea*, perhaps *Polygonum viviparum*, and others, are commonly found in snow-patch communities today and one is tempted to conclude from their presence here or elsewhere that snow-patch communities are indicated at these sites in Zone III times. But *Salix herbacea* in Scotland today may take advantage both of prolonged snow cover and of extreme exposure (often accompanied by solifluction) both of which result in the persistence of open communities (McVean, 1958). Hence ' caution is necessary . . . in using individual plant species as indicators of winter snow accumulation . . . ' (McVean, 1958 : 197). It is not possible therefore to decide to which community *Salix* finds belong unless, as at Whitrig, the extremely small size of many of the leaves can be taken as an indication of exposure. In Norway *Salix herbacea* is characteristic of snow beds at lower alpine levels but at higher altitudes it is not so restricted and occurs in more exposed situations (Dahl, 1956). But in Iceland, in a more extreme oceanic climate, besides occurring in snow beds it is widespread in extremely exposed situations even at relatively low elevations. Indeed as well as *Salix herbacea, Polygonum viviparum, Empetrum nigrum* and *Luzula spicata* all have high frequencies in lowland exposed areas (Hansen, 1930). In Iceland too, *Gnaphalium supinum, Veronica alpina* and *Cassiope hypnoides* are recorded from snow-free areas even if rarely, but they are considered as chionophilous in Norway. Thus the more oceanic the climate the less characteristic will species be of snow bed habitats. It is only such species as *Sibbaldia procumbens* that are confined to the snow-beds throughout their range.

Thus to deduce the occurrence of snow-beds from Late-glacial species lists it is necessary to demonstrate the presence not only of species confined thereto (i.e. exclusive species) but as there is a change of such ' exclusiveness ' as one passes to more and more oceanic snow-beds so only consistent ' exclusives ' will suffice. That is in the absence of precise knowledge of the degree of oceanicity or continentality of the site in question, which would alone allow of present-day parallels to be chosen for comparison.

To deduce the degree of oceanicity or continentality of any given Late-glacial site from the species present, again exclusive or marker species must be sought. For example at Whitrig the presence of *Ephedra* is perhaps suggestive of continentality but an assemblage of such species would be more reliable.

Again, where maximum summer temperatures are limiting, exclusive species are needed to distinguish between ' high altitude ' and extreme oceanicity, so that apart from the indication of continentality given by the presence of *Ephedra*, it might be argued that Zone III at Whitrig could have been a period of extreme oceanicity rather than of cold.

Generalized climatic descriptions for the Late-glacial period have been attempted by Manley (1951, 1959). He suggests from geological evidence that for N.W. England the average annual precipitation during Zone III was ' very nearly as great as today ', and in wet years probably somewhat more. It is conjectured that the low temperatures, and high precipitation which is thought to have fallen more frequently than today, would have given a prevailing dampness and much low cloud at all seasons. The nearest present-day analogy is sought ' in the very wet south-eastern fjords of Greenland ' (Manley, 1959).

When possible shifts in the Gulf Stream and changes in the vigour of the general atmospheric circulation (Lamb, 1959) are involved, direct extrapolation of climatic patterns becomes impossible : the botanical evidence needs to be built up from increasingly complete distribution data of the indicator species recorded for each period of the Late-glacial and for which the autecological requirements are critically understood.

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8. ON THE STUDY OF GLACIAL AND INTERGLACIAL INSECT FAUNAS

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In this paper I propose to discuss some of the problems associated with the interpretation of insect remains found in the glacial and interglacial deposits of this country. These remains are often abundant in peats and in the silts that accumulated in pools or river channels. Most frequently disarticulated skeleton parts are preserved, but in peat or deposits of felted vegetable debris almost complete animals may be occasionally found. In river deposits the remains are often very broken but in silts accumulated in standing water and in peat, the individual skeletal elements are often complete and may retain hairs and scales and even colours. In peats and similar deposits that have undergone compaction the insects are frequently crushed, but in sandy deposits very little distortion occurs.

Though techniques of extraction of insect remains do not come within the scope of this symposium, they have important bearings on the significance of the results obtained and it is, therefore, proposed to mention briefly here the chief methods used. When dealing with peats or felted accumulations of vegetable matter, it is often impossible to break down the material so that insect remains can be concentrated. The most productive method for deposits of this type is to split the material along bedding planes and search the surfaces with a low powered microscope. A great advantage of this method is that associated fragments can be removed and mounted together. However, many of the smaller species are either not noticed or very under-collected and there is a much greater likelihood of the more conspicuous species being over emphasized.

In silts and sand it is often difficult to find insect remains without first concentrating the plant and animal debris. After being broken down, the silt is washed through a series of sieves and the residues are then sorted under a binocular microscope. Most insect remains are found in the fractions retained by the sieves with 50 meshes to the inch or less. The advantages of this method are that it is much less subjective and a much higher proportion of the small and inconspicuous species are obtained. However, any associations that the fragments might have had in the deposit are usually lost. On occasions, however, heads and thoraxes or pairs of elytra of coleoptera may still be found attached together.

Keys to the identification of modern insect species rely on the availability of the entire animal. Only occasionally, therefore, when a more or less complete specimen is found in peat, can these keys be used. When fragmentary remains only are available, however, identifications can be made by matching the fossil specimens against comprehensive modern collections. In this way identifications of varying degrees of certainty can be made according to the number and variety of the fragments available. In many cases only certain parts are diagnostic and the rest of the animal could be assigned to a number of species. However, if some of these more nondescript fragments are found associated together, it is occasionally possible to identify them.

Identification of fossil insects is further complicated by post-mortem changes that may affect the fragment whilst it is buried and also as it dries out after collection. These changes often include an accentuation of the puncturation and deepening of the striae on the elytra of coleoptera and occasionally the development of spurious colours in such genera as *Dytiscus* and *Hydrobius*. These colours often take the form of quite startling vivid blues and greens. Allowances, therefore, must be made for these factors when matching fossil specimens with their modern counterparts.

Deductions concerning the habitat and climatic requirements of a fossil fauna can be made from a simple list of species built up in this way, but the relative abundance of the species is of greater ecological importance. When dealing with insects, each of which is made up of a large number of different skeletal parts, it is often difficult to assess the numerical representation of a particular species. Rarely have all the parts of the animal an equal chance of being preserved. Those which are black or made up of tanned chitin are more resistant to the agents of decay than those which are less well chitinized. Thus, in an interstadial deposit from Upton Warren in Worcestershire, *Helphorus aquaticus* was represented by 64 heads, 192 pronota, 17 left elytra and 14 right elytra, and from a similar deposit at Chelford, Cheshire, *Staphylinus erithropterus* was represented by 14 heads, 6 pronota, 4 left elytra and 3 right elytra. In both these species the elytra are somewhat frail and consequently much more liable to become fragmented. However, the heads of coleoptera have usually less chance of being preserved in a recognizable form than, say, the elytra. Thus, in the Chelford deposit, *Feronia nigrita* was represented by 1 head, 57 pronota, 71 left elytra and 67 right elytra. In this case, the crushed and fragmentary heads were not only hard to find but also difficult to identify with any degree of certainty. Those skeletal elements that are black or brightly coloured have a greater chance of being found than those which are less conspicuous ; thus in the species *Helophorus aquaticus*, quoted above, the head and thorax are brilliantly metallic and much more conspicuous than the filamentous elytra. Lastly, when the insect fragments have been extracted and mounted only some will be sufficiently characteristic to be specifically identifiable.

In the organic silt at Chelford, Cheshire, investigated by Simpson & West (1958) and by Coope (1959), abundant remains of coleoptera were found. These were most frequently found in a felted mass of vegetation and had, therefore, to be extracted by splitting the material and searching the bedding planes. Over ninety species were recognized, some of which occurred in considerable numbers. The frequency of each species is shown in graphic form in Fig. 1. In this graph a vertical line is erected for each species proportional to its apparent abundance and the species are then arranged with the commonest on the left hand side and the rarities on the right. The number of individuals of any particular species has been shown as the highest number of any of its single skeletal elements. Thus the number of individuals of *Feronia nigrita* is taken as 71, since that number of left elytra were recorded. It is admitted that this method of estimating numerical importance will most probably under-represent the commoner species. To avoid confusion only the twelve most abundant species are named on the graph.

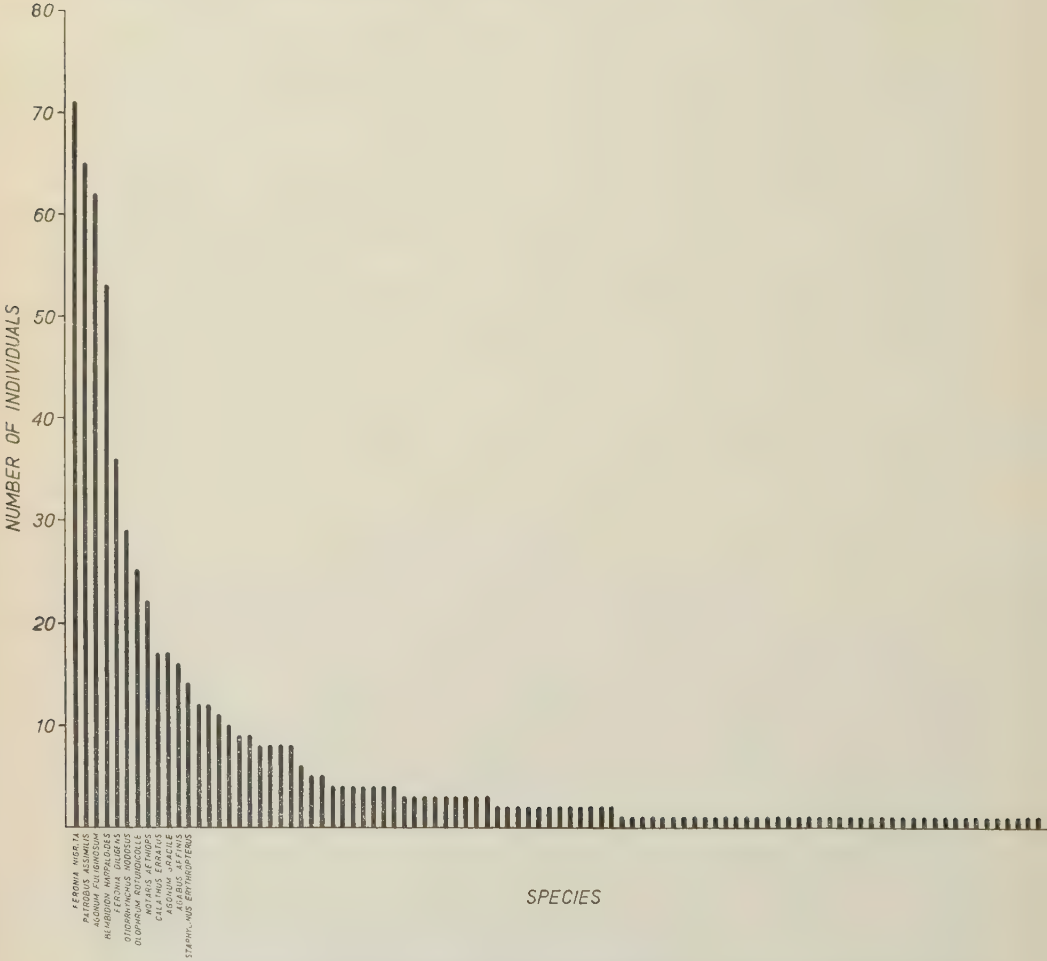

FIG. 1.—Graph showing the apparent relative abundance of species of coleoptera in an interstadial organic deposit at Chelford, Cheshire. Numbers of individuals of a species are represented by the maximum number found, of any diagnostic skeletal element.

When this graph is examined critically it will be seen that the most abundant species tend to be those which are large, black and shiny and, consequently, conspicuous. It is true that *Bembidion harpaloides* and *Olophrum rotundicolle* are fairly small but they were none the less conspicuous in the deposit. Those species that are poorly represented include many that are small and difficult to find and that are thus very much under collected. The varying conspicuousness of some species in the Chelford fauna undoubtedly affected their apparent relative abundance. In Fig. 1, therefore, though the abundance of a species may be indicative of commonness, the poor representation of a species is not necessarily an indication of its rarity in the original fauna.

These, therefore, are some of the reasons that have led me to a more qualitative approach to Quaternary insects in contrast to the essentially quantitative approach of palynology and recent studies of Quaternary molluscs. The insect faunas, however, and in particular the coleoptera, are very sensitive in their response to changes of environmental or climatic conditions and because also of their abundance they have become valuable assets in the elucidation of quaternary ecologies.

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9. THE ECOLOGY OF THE COLEOPTERA FROM SOME LATE-QUATERNARY DEPOSITS

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This paper is intended to illustrate the type of ecological conclusions that it is possible to draw from a study of the coleopteran remains contained within organic deposits laid down during the late-quaternary period.

The coleopteran remains were obtained from vertical monoliths brought back from the sites to the laboratory in ammunition boxes. This method, which preserves the stratigraphical relationships of the material in the deposit has been used to obtain samples for radio-carbon-dating (Godwin, Walker & Willis, 1957 ; Godwin & Willis, 1960). From each ammunition box I have taken three samples for pollen-analysis, at positions of a quarter, half and three-quarters of the vertical depth. In this way it has been possible to :

(a) ascribe the material to its position in the general scheme of the Post-glacial vegetational history of the British Isles (Godwin, 1944 ; 1956) ;
(b) obtain some idea of the vegetational background against which each assemblage of coleopteran remains should be considered.

It had initially been intended that the flotation method of Ladell (1936) and Salt & Hollick (1944) should be used to collect the Coleoptera from the material. However, preliminary experimental investigations, using various combinations of the flotation mixtures recommended by the last-named authors failed to give satisfactory results. The principle difficulties were the large quantity of small plant material which is not separated by this method, and also the increased chances of fragmentation of the sub-fossil material, which is already very fragile (cf. Macfadyen, 1953).

In order to develop these techniques use was made of a monolith obtained from Holme Fen. The results of the pollen analyses from this may be summarized as follows :

(i) the presence of *Tilia* in quite large quantities throughout ;
(ii) the presence of *Fagus* in three samples ;

(iii) the presence of *Alnus* in large quantities throughout ;
(iv) the presence of a large quantity of the pollen of Gramineae in the basal sample ;
(v) the presence of the pollen of *Sphagnum*, and of that of the ericoid type. In both these cases there is a pronounced increase in the percentage representation from the base of the series to the top.

From the first three of these features one may conclude that the material is of fairly recent origin, and probably from Zone VII of the general British scheme. The high value for Gramineae in the basal sample may indicate that this material is from Zone VIIa, whilst the increase in the percentage representation of the pollen of *Sphagnum* and of the ericoid type may be taken as an indication of the developing raised bog.

The next problem which faces one is the extent to which the coleopteran remains are in keeping with what one would expect from a natural population or the remains of one. This is of course a question to which it is ultimately impossible to give a definitive answer. However the results of Williams (Fisher, Corbet & Williams, 1943 ; Williams, 1944) have shown that the collection and analysis of samples of a large number of organisms from a variety of habitats give results which conform to what one would expect if the frequency distribution of the organism conformed to a logarithmic series. With this premise the number of species obtained by doubling the number of samples should be constant in a natural population. To investigate this the number of species obtained from Holme Fen was plotted against the logarithm of the number of samples and also against the logarithm of the number of specimens. In this case, and in the graphs obtained by plotting the same relationships for the data obtained from the site at St Bees to be considered below, the results of the analysis conform to the expected straight line relationship. The remains of the Coleoptera may therefore be said to conform to the expectation of a natural population.

It may now be questioned whether the coleopteran remains reflect the general pattern of continuous change of the vegetation with time, which is suggested by the pollen-analytical results. In order to investigate this it is necessary to compare the composition of the various samples of coleopteran remains. Should the differences of composition represent the effects of random sampling upon a population which is in fact homogeneous with time, then the similarity of two samples should be unrelated to their position in the series. If on the other hand the results represent continuous change then the similarity of two samples situated close together in the series should be greater than between two samples widely separated in the series. To compare the samples the methods developed by plant and animal ecologists have been used (Whittaker, 1958). The first consists of the so-called ' Coefficient of Community '. This compares two samples in terms of the species common to them both :

$$\text{Coefficient of Community} = \frac{c}{a + b - c}$$

where c = number of species common to the two samples,
a = number of species in sample A,
b = number of species in sample B.

This method tends to exaggerate the effects of sharing species with a low numerical representation. To offset this the so-called ' Percentage Similarity ' has been used.

$$\text{Percentage Similarity} = 100 - 0{\cdot}5\ \Sigma\ (a - b)$$

where a and b = the percentages of samples A and B represented by a particular species.

The results of calculating these two coefficients for the data of Holme Fen are shown in the Kulczynski triangles of Fig. 1. It will be seen that the ' Coefficient of Community ' results are largely equivocal, although there may be an aggregation of low values in the top right hand corner which would suggest a greater similarity between neighbouring samples. On the contrary, the results of the ' Percentage Similarity ' show a distinct gradation in which the samples are generally more similar to those close to them in the series than to those more distant from them. To this extent it may be said that the results conform to what would be expected on the basis of the pollen-analytical results.

The percentage representation of the individual specimens of the genus *Hydroporus* and of the *Plateumaris sericea* type confirm this. The specimens of the former occur in large numbers at the top of the series and those of the latter in the bottom of the series. However in the absence of information from elsewhere in the region of Holme Fen it is impossible to decide to what extent this represents a local, and to what extent a wide-spread change. Although the presence of *Hydroporus* in the region of the deposit ascribed to the developing raised bog is of great interest it is in the next deposit, from St Bees, West Cumberland, that we have information upon the extent of the changes observed.

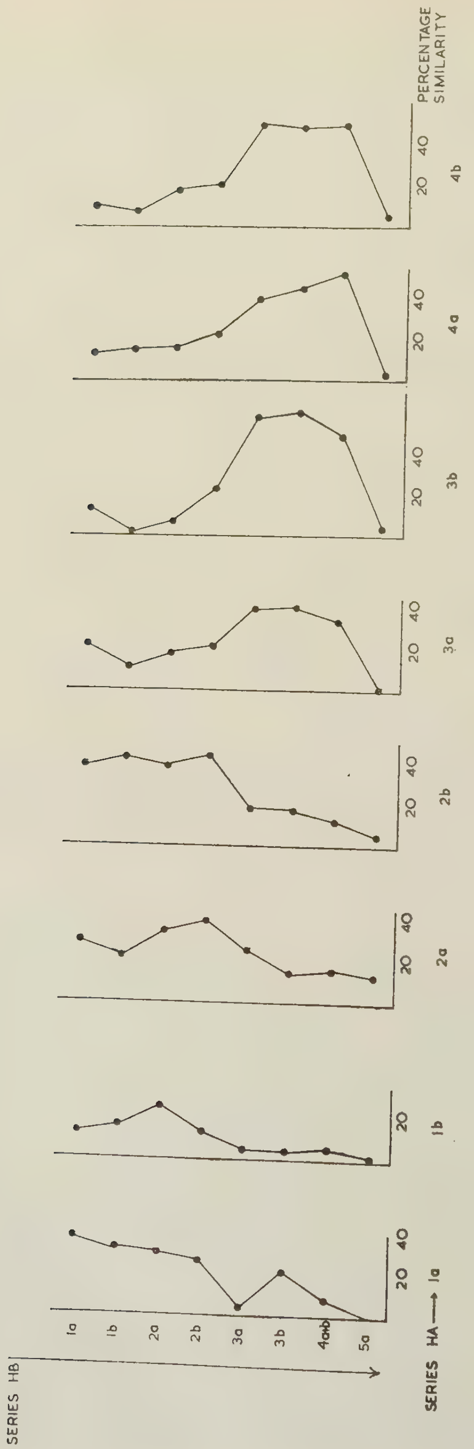
The deposit at St Bees is an organic detritus mud embedded in sands. It was investigated palynologically by Dr Walker, of the Sub-department of Quaternary Research, Cambridge (Walker, 1956). From this deposit I subsequently obtained two monoliths. One was taken from the shallow lateral region and the other from the deeper central region of the deposit. The results of the pollen-analytical analysis of samples from the monoliths were similar to those of Walker. The following important points are of especial interest.

(i) The presence of large quantities of the pollen of herbaceous plants is the upper and lower samples.
(ii) *Betula*, *Pinus* and *Salix* are the only arboreal pollen types present.
(iii) The upper part of the longer series is not present in the shorter series. This upper material must either be of more recent age than that of the shorter series, or, alternatively, the longer series has undergone less compaction.

The first two features outlined above are suggestive of the Late-glacial age suggested by Walker, for the deposit. This age is corroborated by the radiocarbon analysis of wood from the upper part of the longer monolith. This gave an age of 8500 B.C. which would be in agreement with the statement (iii) above.

The results of calculating the ' Percentage Similarity ' of the samples within the two series are shown in Fig. 2. It will be seen that the similarity of the one series is greatest to those at approximately the same level in the other series. To this extent one may conclude that the results obtained in the two series are in agreement and that the changes observed are representative of changes occurring over the entire surface of the deposit. This is further corroborated by the distribution of the specimens of the species *Barynotus squamosus* var. *schonherri* Zett., and *Adoxus obscurus* L. In both series these occur in large quantities in the basal samples and are absent from the upper ones. Conversely *Otiorrhynchus nodosus* F. occurs in large quantities in the upper samples of both series and is absent from the lower samples.

These results are of especial interest ecologically. The Curculionid *Barynotus squamosus* is characteristically a species associated with low herbaceous vegetation beside streams, and in the more southerly regions of its distribution is characteristically montane. This correlates extremely well with the high percentage of the pollen of herbaceous plants noted above. The Chrysomelid *Adoxus obscurus*, which is not recorded from the British Isles at the present time,



PERCENTAGE SIMILARITY OF SERIES HA, AND HB, ST BEES

FIG. 1.

also occurs on herbaceous vegetation and principally upon *Epilobium* the pollen of which occurs sparingly in St Bees.

In contrast to the two former examples *Otiorrhynchus nodosus* is usually associated with woods of *Pinus*. As has been said, it occurs only in the upper samples of both series. This is in striking agreement with the fact that the pollen of *Pinus* is restricted to the upper samples. A similar distribution was also obtained for the Carabid *Patrobus assimilis* Cd., which, although a widespread eurytherm is principally associated with the boreal pine woods in Scandinavia.

It is now of interest to attempt to reconstruct the development of the pond fauna during the period of the deposition of the material. The basal sample of the longer monolith contained a large percentage of dipteran puparia. There were also, in both series, large numbers of the larger Carabidae in the basal samples. These two facts taken together suggest that at this level the deposit represents material which accumulated under damp terrestrial, rather than open-water, conditions. Above this level there occur the cases of the larvae of the Limnophilid/Leptocerid type Trichoptera. Although the fact that there are stenothermous, eurythermous, stenohaline and euryhaline species of these two families prevents one from drawing definite conclusions, nevertheless these animals do comprise a large percentage of the fauna in the clear, often dystrophic, pools in the morraines of the Scandinavian and Alpine regions. Above this there is, in both series, a gradual increase in the percentage representation of the aquatic genera of Coleoptera. This may be taken as an indication of the gradual development of open-water conditions. All the changes within the deposit can, in fact, be correlated with an increase in depth and open-water conditions together with a change from relatively dystrophic conditions to more eutrophic conditions. As an example of this one may consider the relative occurrence of the pollen of the two types of *Myriophyllum*. *Myriophyllum alterniflorum* is predominantly associated with oligotrophic conditions whilst *Myriophyllum spicatum* only occurs where there is at least some calcium in the water. The relative abundance of the two types of pollen grain is shown in Table I.

Coefficient of Community values for the Holme Fen samples

1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	
	16	11	16	22	11·5	16	15·5	8	14	8·5	9	1a
		5	10	11	5	11	15	11	13	12	6	1b
			30	17	16	17	15	25	20	12	0	2a
				7	10	5	5	1.	20	6	0	2b
					22	25	22	12	23	13	15	3a
						22	15	11	21	12	14	3b
							16	19	14	21	15	4a
								23·5	29	5·5	6	4b
									25	23	17	5a
										18	10	5b
											9	6a
												6b

Percentage similarity of samples from Holme Fen

1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	
	28	50	33·5	53·5	47·5	8·5	13	7	16	7	7	1a
		52	51	31	42	36	17·5	33	9	25	5·5	1b
			64·5	50	59·5	33	40	52	18	38	6	2a
				43·5	59·5	37	32	29	18	25	0	2b
					71·5	22·5	20	13·5	21·5	13·5	3·5	3a
						42	29·5	22·5	21	22·5	8·5	3b
							31	25	21·5	31	12	4a
								38·5	12	25	6	4b
									39	57·5	33	5a
										26	30	5b
											47	6a
												6b

FIG. 2.

A consideration of the coleopteran remains from a detritus mud erratic in the valley gravels at Colney Heath, St Albans, is principally of zoogeographical interest. However the pollen analyses from the material are again those of a predominantly open-vegetational community dominated by *Carex* and the Gramineae and with *Pinus*, *Betula* and *Salix* the only arboreal pollen types present. This is of interest in view of the occurrence of *Miscodera arctica* Pk. which is a stenotope characteristically found in open vegetational commu-

TABLE I.—The relative occurrence of the pollen of the two types of *Myriophyllum* expressed as a percentage of the total tree pollen per sample

Pollen sample	Percentage representation of Myriophyllum alterniflorum	Percentage representation of Myriophyllum spicatum
4	...	24
5	380	640
6	75	595
7	102	...
8	1700	5
9	2100	...
10–15	Myriophyllum alterniflorum only	...

nities on morrainic ground. The presence of large quantities of *Notaris aethiops* is in conformity with the occurrence of large numbers of *Carex* remains as this Curculionid is typically found in Cariceta. The occurrence of *Dorytomus salicinus* Gyll is also in agreement with the presence of *Salix* remains.

It is of interest to mention briefly the zoogeographical characteristics of the various faunas. That of Colney Heath, which is the oldest of the sites considered here, and whose age, as determined by radio-carbon analysis is approximately 12,000 years B.C. (Godwin & Willis, 1960), includes many widespread eurytherms, but also stenothermic arctic or high boreal species. These either have a limited montane distribution in the British Isles at the present time e.g. *Patrobus septentrionis* Dej., or do not occur here e.g. *Diachila arctica*.

The stenothermous element in the Late-glacial deposits at St Bees, is smaller. There is still the large number of widespread eurytherms, but alongside these are the remains of the species *Adoxus obscurus* L., and *Tomocarabus convexus* F. Neither of these occurs in the British Isles at the present time and *Tomocarabus convexus* has a distinctly continental distribution.

The fauna of Holme Fen is similar to what one would expect to find in similar conditions at the present time.

These results substantiate the conclusions of the Danish entomologist Dr Kai Henriksen in his investigation of the history of the Danish Coleoptera Fauna. In view of this one may conclude that species which have a restricted or disjunct distribution in the British Isles, had a wider and more southerly distribution during the Late-glacial period. In consequence one must look for the causes of their subsequent restriction in the warmer conditions and afforestation of the Post-glacial period. This conclusion parallels that reached for the montane and disjunct components of the British Flora.

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10. THE ECOLOGICAL INTERPRETATION OF QUATERNARY NON-MARINE MOLLUSCA

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INTRODUCTION

NON-MARINE mollusca are one of the most common groups of fossils in Quaternary deposits, rivalling ostracods and macroscopic plant remains in their frequency. They are preserved in a wider range of sediments than fruits and seeds, because they will withstand oxidation, although leaching soon removes them. Further, they have been studied for at least a century, while a lot is known about the present day ecology of many of the species, owing primarily to the number of naturalists who have been interested in snails. These reasons are sufficient for an attempt to explore fully their use in Pleistocene ecological reconstructions.

SAMPLING

Many museums up and down the country contain handsome specimens of the larger species of land and freshwater mollusca, which have been recovered from Quaternary deposits. Although much energy has been put into the collection of such specimens, a lot of collection has, unfortunately, been done regardless of exact horizons and of the desirability of obtaining representative faunas. As botanical work has shown the surprising extent of the changes occurring even in a few centimetres of sediment, it is obviously desirable to put the collection of mollusca on a similar precise basis. This means very careful stratigraphy and the accurate assessment of the proportional representation of species in the fauna.

The most useful sample of material is one of about 2 to 4 pounds weight, for, if this does not contain sufficient mollusca, it may be concluded that they are probably too infrequent for analysis in the deposit. At the same time it is a satisfactory sample for the recovery of fruits and seeds, which may be picked out at the same time as the mollusca are being sorted. In open sections, the thickness of sediment in one sample need not exceed 10 cm., or even half of this if the material is rich in fossils, for a detailed analysis to be made. With cores, which are often necessary to sample important but inaccessible deposits, the intervals for analysis must obviously be governed by the diameter of the core and the frequency of fossils. In view of the fact that with most types of percussion corers, whether civilized and driven in by a motor or primitive and driven in with a sledge-hammer, there is the risk, unless the bore is cased, of material being scraped down as the corer is re-inserted, cores have usually been divided into a bottom half and two upper quarters. Contamination will then be in the top quarter, which can be ignored if there is strong reason for suspecting contamination. In practice serious contamination seems to occur very infrequently.

Any attempt to pick out shells by eye from a deposit is bound to lead to distortion in the percentage frequencies of species. If one walks across the interglacial deposit on the foreshore at Selsey, Sussex, the frequency of valves of *Corbicula fluminalis* would probably be assessed at about 20–40 per cent of the total. However, if all the valves, including those of juveniles of no more than 1–3 mm. diameter, are counted, and, in addition, all fragments of valves containing recognizable hinge teeth are also counted as valves, the frequency does not exceed 1·5 per cent of the total mollusca. Unfortunately, one cannot do an unprejudiced test of one's own sorting abilities for fear of unconscious efforts to guard against bias in visual selection, but I have been recently given, through the kindness of Dr John Alexander, a series of shells picked out by eye from a buried soil beneath a Bronze Age barrow at Arreton Down, Isle of Wight, and a bulk sample of the same material. The frequencies obtained from the two samples are shown in Fig. 1: they are very different, for *Vallonia costata* amounts to 53·2 per cent of the fauna from the bulk sample and only 2·3 per cent of the selected series. The large shells, *Helicella itala, Helix* (*Cepaea*) spp. and *Pomatias elegans*, the major dimensions of which are shown to the left of the histogram, are, as might be expected, those selected by eye. Colour also plays a part, as *Pupilla muscorum*, almost the same colour as the containing buff loam, was not selected visually. The failure to select this last species by eye was also true of another pair of samples I have from the same site. The differences between the faunas obtained by selection and from bulk samples may be even greater than shown, for the series of snails selected during excava-

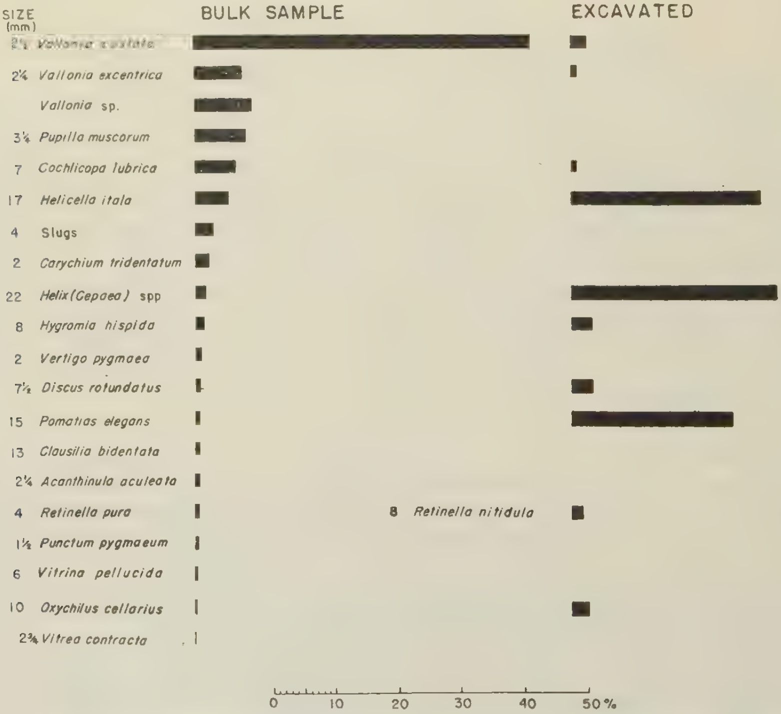

FIG. 1.—Comparison between faunas derived from the soil beneath a Bronze Age barrow at Arreton Down, Isle of Wight, by bulk sampling and visual selection.

tion was washed and some of the small species may have been contained in the matrix encrusting and within the larger shells. Fortunately, in the example given the ecological interpretation was not greatly affected by the bias of the visually selected series, but it might well be in other cases. Selection by eye is still important in obtaining a comprehensive fauna of good specimens from a site, for cores and other bulk samples usually yield battered material best kept out of sight rather than displayed in a museum. Again some of the larger species may well be missed in bulk sampling, but the error so involved is far less than the missing of smaller species in visual selection.

Sorting and Counting

It is my practice to be rather brutal in washing down sediments for much of the broken material is already crushed in the sediment. Vigorous swirling of the sediments in sieves in a sink of water and, in desperate moments, strong jets of water to break very clayey sediments, have been used. These do not seem to have very destructive effects if one may judge, apart from the mollusca, from the fact that delicate plant remains, such as *Carex* nutlets with utricles, seem to be recovered in very much the same proportions after such treatment as with more refined washing methods. In addition large numbers of delicate seeds, such as those of *Zannichellia*, *Naias minor* and winged *Betula*, are recovered intact. Of course, if the sediment breaks down readily for example a silt which has been thoroughly dried and then re-wetted, it requires and should get only the gentlest washing, but if it is very compact, in spite of preliminary soaking in caustic soda or potash solutions, it is better, in my opinion, to risk a little damage in order to wash away as much of the matrix as possible.

The residue is then dried and sifted dry into fractions of over 2 mm., 1–2 mm., $\frac{1}{2}$–1 mm. and $\frac{1}{4}$–$\frac{1}{2}$ mm. The largest grade is sorted by eye or with a hand lens on a black glass plate, the next two are sorted by sprinkling the material thinly on a lined porcelain plate, so that it may be systematically scanned with a low-power binocular microscope. All snails, seeds, fruits, beetle and weevil fragments and small vertebrate remains may then be picked up with a moistened brush. The smallest grade, $\frac{1}{4}$–$\frac{1}{2}$ mm., is preserved, usually to see whether it contains small fruits and seeds, for example those of *Typha*, *Juncus* and *Hypericum*, and to estimate the frequency of very small organisms, for example the oospores of *Chara* spp. and the tests of foraminifera, but it has been found unprofitable to try to identify mollusca fragments at this very small size. It can be done for a number of species, but so many species are no longer identifiable that there is a danger of distorting the frequency diagram. Furthermore sorting is an incredibly tedious task, for, without looking at anything smaller than $\frac{1}{2}$ mm. one might well use up all one's spare time for a fortnight in sorting a very rich sample. As any given deposit may well be divided into 20–40 samples, it can be seen that thoroughness can be overdone.

One virtually obtains, then, a percentage frequency table of all species of mollusca, the fragments of which exceed $\frac{1}{2}$ mm. in diameter. Counting is usually best done on apical fragments, but on apertures where they are diagnostic e.g. in the genera *Carychium* and *Vertigo*. It is my custom to count valves of lamellibranchs as individuals, for the small genera, especially *Pisidium*, are readily crushed and difficult to identify when immature, while the large genera, especially *Anadonta* and *Unio*, are often either crushed in the sediment or fall into a mass of useless irridescent flakes when washed down. Thus, a count of valves as individuals probably does not greatly distort the percentage frequencies of the species. Nevertheless, those percentages do not reflect precisely the original percentage representations of the species. This is due to the number of very fragile shells which must be destroyed e.g. *Succinea* spp., *Lymnaea glutinosa* and some Zonitidae, and to the virtual impossibility of separating some species on apices. The method really depends on the experience of the operator in identifying fragments—and it is surprising what differences may reveal themselves with experience—but there is still a residue of broken material only generically or sub-generically identifiable e.g. the following pairs and groups are almost impossible to tell apart: *Succinea putris* and *pfeifferi*; *Planorbis planorbis*, *carinatus* and *laevis*; *Vallonia pulchella* and *excentrica*; the species of *Agriolimax* and *Limax*; *Cochlicopa lubrica* and *lubricella* (and *nitens* if it occurs in our Pleistocene); and some Clausiliidae. However, painstaking work in the past has made it possible to identify with increasing confidence smaller and smaller individuals and it is to be hoped that, as more time is devoted in the future to typical broken Pleistocene material, more of it will be specifically identifiable.

The size of the sample used usually means that at least several hundred, and often several thousand, mollusca are recovered. No attempt has been yet made to select a sample count as in pollen analysis, for the material is usually obtained with such difficulty that it would be folly not to make as exhaustive an examination of the fauna as possible.

Interpretation

In Quaternary research it is desirable to be able to interpret the local environmental conditions from the mollusca found in deposits as well as to infer the general character of the climate from the same evidence. Interpretations of climate always involve an assessment of local conditions, for the effects of changes in these local conditions have to be discounted. Hence the interpretation of local conditions is the first step. Depending on the deposit and the aim of the interpretation, percentage frequencies of single species, genera or whole groups of species may be studied.

The diagram from the Last Interglacial deposit at Selsey, Sussex (Fig. 2) merely shows the percentage of the total fauna formed by the genus *Hydrobia*, and the percentage of the total *Hydrobia* formed by the species *ulvae*. These two show the extraordinarily sharp change from freshwater to brackish conditions near the base and the probable slight increase in salinity betrayed by the increase in *ulvae* near the top, for this species is usually held to be tolerant of higher salinities than *ventrosa*, though this seems not to apply everywhere. It needs to be taken in conjunction with the presence of *Scrobicularia* at the same levels. Thus, in this example, it is sufficient to use one genus to demonstrate a major and particularly obvious ecological change.

A slightly more complex example is shown in Fig. 3, which depicts the changes occurring after a marine regression in another Last Interglacial deposit at Asnelles-belle-plage in Normandy. Below the level shown the fauna consisted mainly of juveniles of marine mollusca and of foraminifera of inshore types. The change occurring as the area emerged was as sharp as that consequent on submergence at Selsey. There appears upon emergence to have been a relief of low swells of marine silt separated by slacks, with freshwater and marsh mollusca living in the slacks and xerophiles on the swells. As sea level continued to fall and the area became better drained, the slacks slowly dried. This interpretation is suggested by the way in which the freshwater genus *Lymnaea* decreases upwards (*truncatula* is excluded because it is virtually a marsh snail); by the upward decrease of *Planorbis leucostoma*, not as marked as in the *Lymnaea* graph because the species will tolerate very poor freshwater conditions; by the increase upwards of the marsh genus *Succinea* and the mainly marsh genus *Agriolimax*; and, finally, by the increase at the very top of the dry-loving *Pupilla muscorum*.

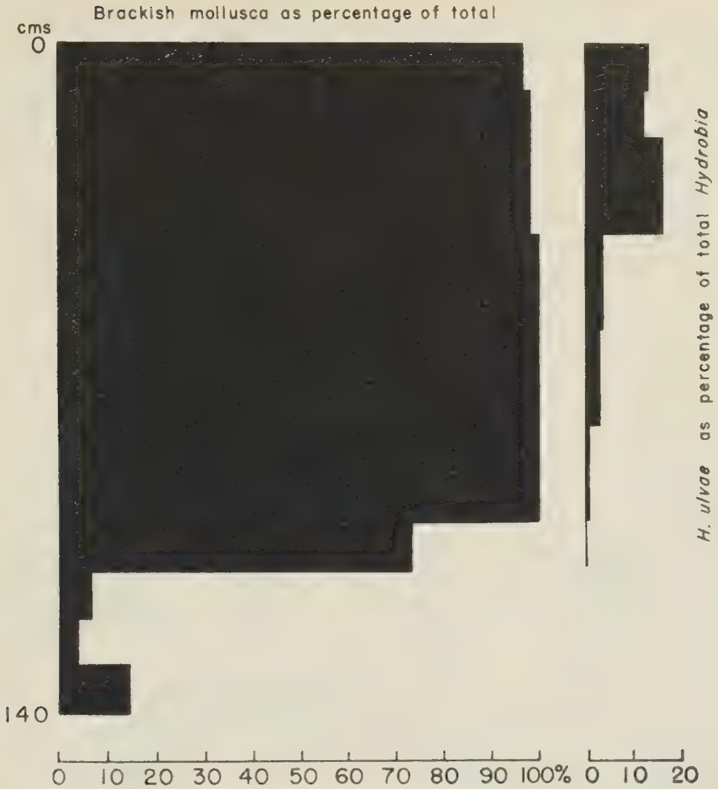

FIG. 2.—Frequency of *Hydrobia* in the Last Interglacial deposit at Selsey, Sussex.

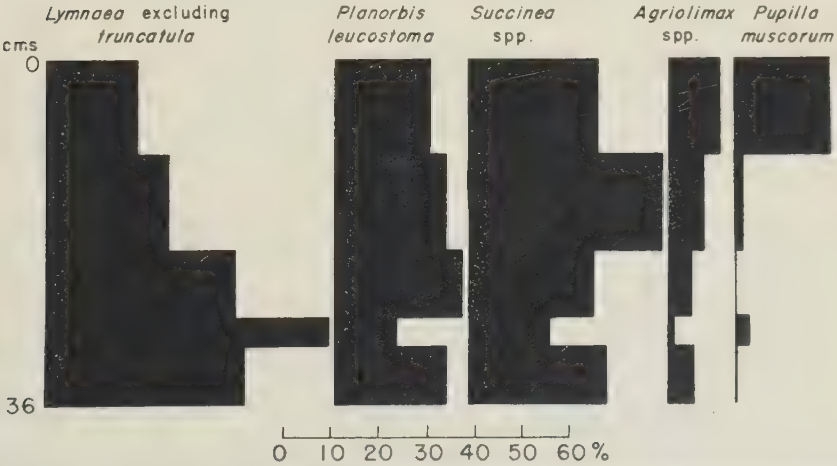

FIG. 3.—Frequency of certain species in the Last Interglacial deposit at Asnelles-belle-plage, Normandy.

A rich interglacial deposit, however, often contains between 40 and 80 identifiable species, so that graphs of individual species would result in an extremely complex diagram. It is then necessary to group species. The fundamental division into land and freshwater groups is the first step, but, beyond that, grouping is much more tentative. This is primarily because most mollusca will tolerate a wide range of habitats and climates: it is not unusual to read of a particular species that it is widely distributed from the Arctic Circle in Scandinavia southwards over the whole of western and central Europe into the Iberian and Italian peninsulas, over which range it is found in streams, canals, lakes, ponds and ditches. Such embracing distributions are daunting at first sight, but, ignoring the climatic range for the moment it can usually be said that a given species is most characteristic of certain conditions though it may also be found in many others. On this basis with the aid of the invaluable ecological papers by Boycott and various European faunas, the freshwater mollusca have been divided into the following ecological groups:

1. A slum group. The term, originally used by Boycott, describes well the preference for, or tolerance of, poor water conditions shown by the species concerned. Small bodies of water subject to drying, to stagnation and to considerable temperature variations are the habitats suggested by the group, which includes species such as *Lymnaea truncatula*, *Aplexa hypnorum*, *Planorbis leucostoma*, *Sphaerium lacustre* and the *Pisidium* species, *casertanum*, *personatum* and *obtusale*. The fact that more than one type of poor habitat is included is suggested by the fact that *Pisidium casertanum* and *personatum* are often associated in the same deposit, while *obtusale* usually seems to occur on its own.
2. A catholic group. Under this heading I have included freshwater mollusca which will tolerate a wide range of habitats except the worst slums, for example, *Lymnaea palustris* and *peregra*, *Planorbis crista* and *contortus*, *Segmentina complanata*, *Sphaerium corneum* and the *Pisidium* species, *milium*, *subtruncatum* and *nitidum*.
3. A ditch group. Included here are species which are often found in ditches with clean, slowly-moving water and abundant growth of aquatic plants. They include *Valvata cristata*, *Planorbis planorbis*, *vortex* and *vorticulus*, *Segmentina nitida*, *Acroloxus lacustris* and *Pisidium pulchellum*.
4. A moving water group. Species of this group are more commonly found in slightly larger bodies of water, for example moving streams and larger ponds, where the water is stirred by currents and the wind. The streams may be no more than a few yards wide and no faster than those of East Anglia; no picture of mountain torrents is intended. Mullusca included here are such species as *Valvata piscinalis*, *Bithynia* spp., *Lymnaea stagnalis*, *Physa fontinalis* and the *Pisidium* species, *amnicum*, *henslowanum* and *moitessierianum*, together with the larger bivalves.

The land mollusca have not been so divided, but the following groups have been separated:

1. Marsh and associated species. This is virtually the list given by Boycott with the substitution of *Vallonia pulchella* for *excentrica*.
2. Dry land species. *Vallonia costata* and *excentrica*, *Pupilla muscorum* and *Helicella* spp. are typical of this group.
3. *Vallonia* spp. may sometimes profitably be separated as indicating open unwooded conditions.
4. 'Woodland' species, though difficult to define, may sometimes usefully be considered separately, though conclusions about vegetation are obviously best derived from plant remains wherever these are preserved.

These groups must not be considered in any way final, as the variations in the groups have so far been studied for very few deposits. They may need either revision or expansion ; it is possible to imagine conditions in which it would be advantageous to consider species typical of rapid streams e.g. *Ancylus fluviatilis.*

The practical value of these groups may be shown at Apethorpe, a village near Oundle on the Willow Brook, a tributary of the river Nene. Here a shallow lens of Post-glacial valley fill, mainly detritus mud, makes it fairly easy to infer that the edges of the fill must represent marshy conditions and the central part stream conditions, so that an instructive comparison should be possible between cores taken at the edge and in the centre of the infill. As shown in Fig. 4, there is a far higher proportion of freshwater mollusca in the central than in the marginal core. Further, the central core has mainly the moving water and catholic groups of freshwater mollusca plus a fairly high proportion of ditch species while the marginal core has almost entirely slum species. The land mollusca do not show such great differences, although the marginal core does show more ‘ woodland ’ species, a fact not recorded in the figure. The similarity of the uppermost parts of both cores is due to a change to a mottled brown clay in each core, this probably representing flood silt deposited by streams draining cultivated land.

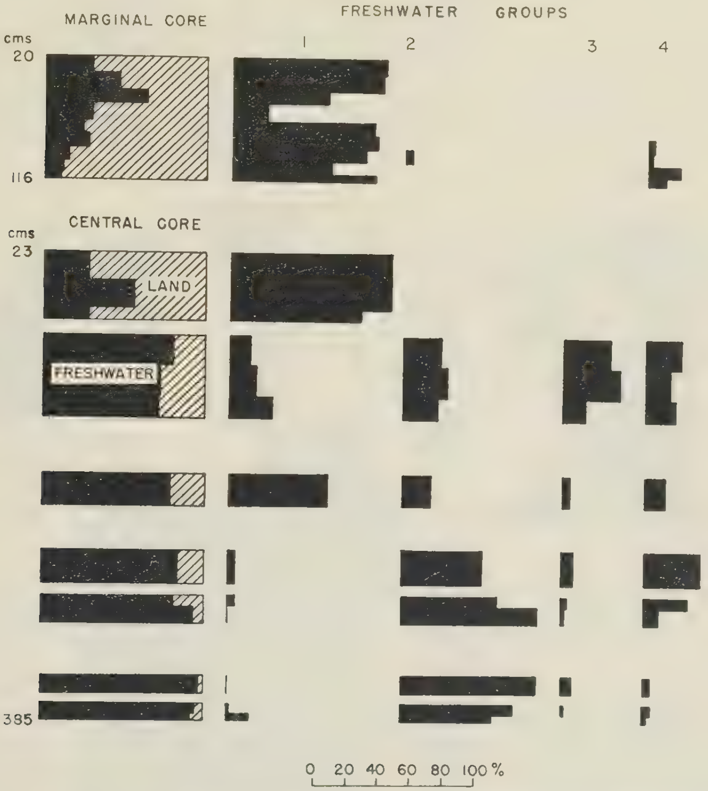

Fig. 4.—Frequency of land and freshwater mollusca in the Post-glacial deposit at Apethorpe, Northamptonshire. The freshwater groups, numbered as in the text, are shown as percentages of the total freshwater mollusca. Gaps in the central core are due to sampling difficulties.

Unlike Post-glacial deposits, such as that at Apethorpe, interglacial deposits do not often readily reveal the central and marginal parts of infillings, so that the interpretation of local conditions rests solely on the fossils. The use of these groups was tested on the Last Interglacial deposit at Histon Road, Cambridge (Sparks & West, 1959) and variations through part of this deposit are shown in Fig. 5. In the first section, A–B, conditions are marshy at the base, A, as shown by the dominance of the slum freshwater group and by the marsh land group. From A to B the slum group declines, the catholic and ditch groups reach successive intermediate peaks, while the moving water group reaches its peak at the top, B. At B, stream conditions are fully established and last until C ; they are characterized by the dominance of moving water and catholic freshwater groups and by dry land species. The latter may seem surprising, but many of these shells have small apertures and float easily when the aperture is full of dirt, so that the rivers readily move them downstream. At C there is an abrupt reversion to marsh as is shown by the great increase of the slum freshwater group and the marsh land group, while at D there is an equally abrupt change back to moving water conditions, this time with so few land mollusca as to make it not practicable to graph them. The general high proportion of *Vallonia* spp. among the land snails is a suggestion of open conditions confirmed by the botanical evidence from the site. The variations of the different groups both in this deposit and in that at Apethorpe seem to be consistent with a series of interpretable ecological changes.

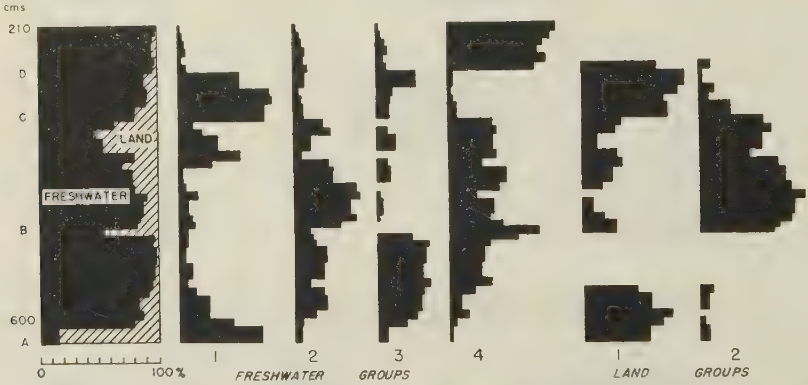

Fig. 5.—Frequency of land and freshwater mollusca in part of the Last Interglacial deposit at Histon Road, Cambridge. The freshwater and land groups, numbered as in the text, are shown as percentages of the total freshwater and land mollusca respectively.

Climatic interpretations may also be based on frequencies of individual species or groups of species. It is only really satisfactory to take individual species in deposits showing minimum changes in local conditions : otherwise changes in individual species are more likely to be due to local changes than to general climatic changes. A Last Interglacial deposit with comparatively uniform local conditions is that at Bobbitshole, Ipswich (West, 1957 ; Sparks, 1957). In Fig. 6, five species with ranges well north in Scandinavia are graphed, then five with ranges reaching only middle Scandinavia (except *L. glutinosa* which extends well to the north), and finally a southern species, *B. marginata*, and the land mollusca as a whole, for the last included a number of southern forms. In spite of the missing section of core, it is clear that the most tolerant species predominate at the base, that the less tolerant species reach an intermediate

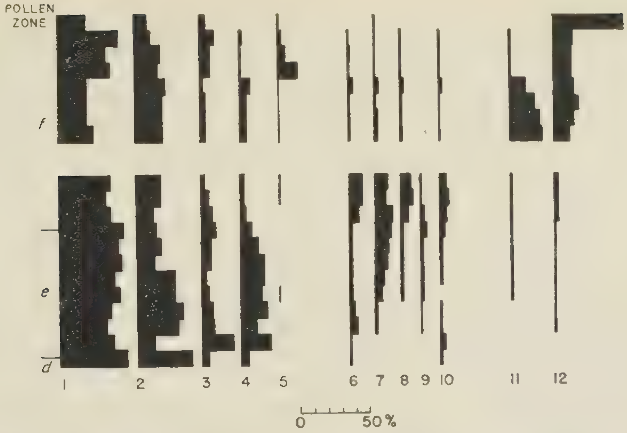

FIG. 6.—Frequency of selected species in the Last Interglacial deposit at Bobbitshole, Ipswich. 1, *Valvata cristata*. 2, *Bithynia tentaculata*. 3, *Lymnaea peregra*. 4, *Planorbis crista*. 5, *Planorbis leucostoma*. 6, *Acroloxus lacustris*. 7, *Planorbis vorticulus*. 8, *Planorbis carinatus*. 9, *Lymnaea glutinosa*. 10, *Segmentina complanata*. 11, *Belgrandia marginata*. 12, Total land species. The gap in the core was caused by sampling difficulty.

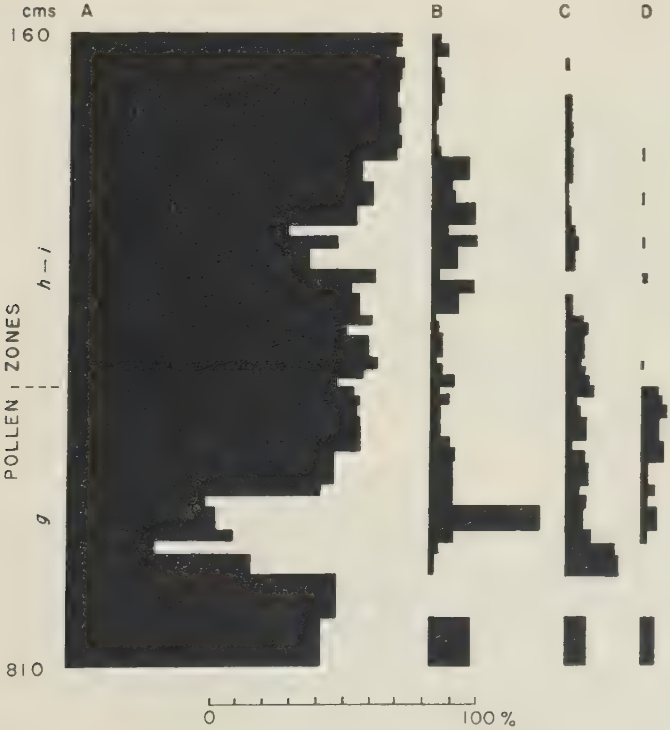

FIG. 7.—Frequency of distributional or climatic groups in the Last Interglacial deposit at Histon Road, Cambridge. The groups are lettered as in the text.

peak and that the least tolerant species reach a peak near the top of the graph, except for a probably ecological complication, when *Planorbis leucostoma*, a species tolerant of poor slum conditions as well as of northern climates, comes in strongly.

On the other hand, a deposit such as that at Histon Road, with its many abrupt changes in local conditions, cannot be treated in the same way, simply because of the way in which the frequencies of species are governed by local conditions. Climatic or distributional groups need to be made and four of these have been selected :

A. Species reaching to or almost to the Arctic Circle in Sweden.
B. Species reaching approximately 63 N. in Sweden.
C. Species reaching approximately 60–61 N. in Sweden, i.e. the approximate limit of the oak.
D. Species only found in the very south of Scandinavia or confined to the European mainland.

It is clear from Fig. 7 that these groups behave as one would expect in a deposit dating from the second half of an interglacial. Groups D, C and B decrease successively upwards, while group A increases its dominance. Thus, by grouping it seems that the changes caused by local conditions may be offset, and that a clear picture of the climatic trend emerges.

Conclusion

From the few examples tested it seems that a reasonable picture of local conditions may be built up from a study of the non-marine mollusca. In most cases these interpretations have been checked against those derived from a study of the plant remains by Dr R. G. West and the results have been remarkably consistent.

The general run of climatic change may also be inferred and some approximation to the actual climate may be attempted, provided that one considers the fauna carefully, especially the fact that even in the middle of an interglacial the fauna is mainly composed of tolerant, widely-distributed species. Too much weight should not be placed on the presence of a few very southern species, e.g. *Corbicula fluminalis*, for discrepancies between past and present ranges may not depend solely on climate, but on factors such as human interference and interglacial and post-glacial possibilities of migration.

Although in the deposits studied there seems to be a marked increase in southern mollusca in the mixed oak forest zone *f*, of the Last interglacial it is probably completely unsafe to attempt to use mollusca like pollen for zoning purposes, because, unlike pollen, the mollusca of a deposit directly reflect local conditions.

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11. INTERGLACIAL AND INTERSTADIAL VEGETATION IN ENGLAND

By R. G. West

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The subdivision of the Quaternary Period is customarily based on climatic changes. Cold glacial stages alternate with warmer non-glacial stages. During these latter stages, vegetational development follows after the retreat of the ice. The degree of development depends on the length of the non-glacial stage, and thus on the time available for colonization by plants, and also on the extent and rate of climatic change during the stage. A distinction is usually made between interglacial and interstadial intervals. In the former the length of the non-glacial phase and the degree of climatic amelioration permit the development of temperate forests indicative of climates at least as warm as during the Post-glacial climatic optimum. In the latter, either the shortness of the non-glacial phase or the small degree of climatic amelioration prevents such vegetational development and only sub-arctic or boreal vegetation occurs. Obviously the variability of the factors concerned does not always allow a clear-cut distinction between these two kinds of non-glacial phase.

In Britain far fewer interglacial and interstadial deposits have been examined than is the case with Late- and Post-glacial deposits, so that generalizations about the vegetational successions shown by them are necessarily provisional. However, we have knowledge of the vegetation of one interstadial phase in the Last Glaciation (excluding the Allerød interstadial at the end of the Last Glaciation, which has been dealt with in detail by other speakers) and of three distinct interglacial stages.

Evidence of an interstadial phase in the Last Glaciation is given by a deposit of organic mud in the Middle Sands of the Cheshire Plain at Chelford (Simpson & West, 1958). Here plant remains showed the presence of *Betula-Pinus-Picea* forest of a kind now found in northern Finland. This coniferous forest must have developed during a retreat phase of the ice from which was deposited the outwash forming the sands both below and above the mud horizon. A radiocarbon dating of wood from the mud gave an age of 57,000 years.

The three known interglacial stages occur as follows in the glacial-interglacial succession (West, 1958) :

  (Post-glacial)
Last Glaciation
  Ipswichian Interglacial
Gipping Glaciation
  Hoxnian Interglacial
Lowestoft Glaciation
  Cromerian Interglacial
(Early Pleistocene Crag Sediments)

Schematic pollen diagrams showing the vegetational changes in south-east England through these interglacials and the Post-glacial are shown in Figs 1 to 4. All show vegetational trends signifying climatic amelioration and then deterioration, with revertence of the pollen curves in the latter half of the interglacial.

Generally speaking, four substages (each including one or more vegetational zones) may be distinguished in the interglacial pollen diagrams :

1. Late-glacial substage, with relatively open vegetation, following soon after the retreat of the ice.
2. Early-temperate substage, in which mixed oak forest develops and dominates.
3. Late-temperate substage, in which the mixed oak forest is replaced by coniferous forest.
4. Early-glacial substage, in which relatively open vegetation replaces forest (this substage is rarely found as cold climate phenomena tend to prevent its formation or preservation).

As will be seen from the figures, each of the three interglacial stages has a pollen diagram characteristically different from the others and from the Late- and Post-glacial diagrams.

Among the Late-glacial substages, that from the Hoxnian is characteristic in having high pollen percentages of *Hippophaë rhamnoides*. Otherwise they are similar, having the characteristic Late-glacial assemblage of herbs, e.g. *Artemisia, Helianthemum, Thalictrum*.

The early-temperate substages of the different interglacials are very different. As an example of these differences, note the differing behaviour of the *Corylus* pollen curve in Figs 1 to 4. In the Cromerian Interglacial, *Quercus* and *Ulmus* are equally well represented in the early-temperate substage. In the Hoxnian, *Quercus* is far more abundant than *Ulmus* and *Tilia*, though both the latter are frequent. In the Ipswichian, *Tilia* and *Alnus*, both present in differing quantities in the other interglacials and the Post-glacial, seem to be very poorly represented in the pollen diagrams. *Ulmus* is slightly more frequent and *Quercus* very abundant. Also, *Acer* and *Carpinus* both form substantial pollen curves only in this interglacial.

In the late-temperate substage there are likewise differences among the interglacials. In the Cromerian *Picea* is well represented : in the Hoxnian, both *Picea* and *Abies* are fairly abundant, and in the Ipswichian there is no *Abies* and very little *Picea*.

I now want to consider some of the factors which might determine these differences in the interglacial vegetational sequences.

First, factors connected with the distances of the glacial refuges of the plants from England and the rates of migration of different species. If the climatic amelioration at the beginning of the interglacial is more rapid than the rate of migration, this rate and the distance of the glacial refuge will affect the time of appearance of, say, the mixed oak forest trees in the interglacial. Difficulties in interpreting the differences in the pollen diagrams as results of this kind of factor arise because often we do not know the species concerned in the pollen diagrams, and because we know little of the biological factors determining the rate of migration. In the absence of palaeobotanical evidence of glacial floras in refuge areas it is difficult to suggest the positions of these areas, though some information may be gained about the direction of migration from a comparison of pollen diagrams of the same age over a large area. Such reconstruction of migrations in the Late- and Post-glacial has been made by Firbas (1949), but has not yet been done for the interglacials.

In the early-temperate substages *Ulmus* and *Quercus* are the first of the thermophilous trees to appear in all the interglacials and the Post-glacial. *Tilia, Alnus* and *Corylus* appear at variable times. As shown in the figure, *Corylus* also behaves differently in the different interglacials and the Post-glacial. Nuts ascribed to *C. avellana* have been found in all the interglacials, so it is probably with this species that we are concerned. Possibly the differing *Corylus* curves result from the behaviour of the species in competition with the mixed oak forest trees, following a different time of arrival of the species. In the two earliest interglacials *Corylus* expands late, well into the mixed oak forest zone, and is not very well represented in the pollen diagrams. In the Ipswichian, *Corylus* expands to high percentages with the mixed oak forest early in the interglacial. Perhaps this early spread is related to the incomplete forest cover suggested by pollen diagrams from this interglacial. In the Post-glacial, *Corylus* appears in quantity before the mixed oak forest and expands to high values before it becomes dominant. As mentioned above, these differences might be a reflection of the differing distances of the glacial refuges of *Corylus* during the successive glaciations. But it is also possible that ecological preferences, or some other properties of the species affecting its competition with the mixed oak forest trees, have changed during the long period covered by these interglacials.

In the case of forest trees appearing later in the interglacials still other considerations arise in the interpretation of the differences between the interglacials. The conifers of the late-temperate substages are replacing the mixed oak forest trees, either as a result of climatic change, or possibly as a successional change following soil changes as the interglacial proceeds.

The second kind of factor to be considered is that of barriers to migration of plants into Britain, in particular, the effects of sea-level changes in the interglacials. In the Post-glacial, and in each interglacial, Britain would be cut off by a eustatic rise in sea-level as the ice melted, providing that the Straits of Dover were in existence. The time of the rise in sea-level in relation to the development of the vegetation is obviously of importance in determining the course of its development. In the Post-glacial, the rising sea-level (see Fig. 4) seems to have cut off Britain from the continent at some time during the Boreal period (Zone VI). As an example of the effect of isolation by a rising sea-level on plant distribution, we may mention the two trees, *Tilia* and *Fagus*, which, though present in England, were prevented by the rise from further migration to Ireland, where they are not found native in the Post-glacial. In the Ipswichian Interglacial there is evidence that sea-level rose above its present height in the temperate substage (in Zone *f*, see Fig. 3), relatively earlier than in the Post-glacial. It is possible that this early rise may account for the differences between the continental and English Ipswichian interglacial pollen diagrams, e.g. the apparent lack of *Tilia* in England though it is common on the continent in this interglacial. On the other hand, in the Hoxnian Interglacial, there is some evidence that the rise above present sea-level was much later, late in the early-temperate substage or in the late-temperate substage, and this may account for the similarity of the late-temperate substage vegetation in England and on the continent, with both *Abies* and *Picea* as prominent conifers. An alternative explanation for the similarity is that a land bridge with the continent existed in this interglacial, the Straits of Dover being fully cut in the subsequent glaciation.

The sea-level changes of the older interglacials, however, are difficult to investigate as tectonic changes have considerably affected the North Sea area.

Lastly, I want to consider climate as a factor determining the differences in the interglacial vegetational successions. It is difficult to distinguish the effects of climate in detail. The arrival and spread of species are not necessarily correlated with climatic change. If the rate of climatic change is faster than the rate of migration of the plants, the presence of a species gives a ' minimum ' value for climate. As we have seen, the vegetational succession can obviously be determined by factors other than climatic change. Where the vegetation type shown by the pollen diagrams remains stable, general indications of climate, e.g. degree of oceanicity or continentality, may be obtained. Where the disappearance of species can be correlated with climatic amelioration or deteriora-

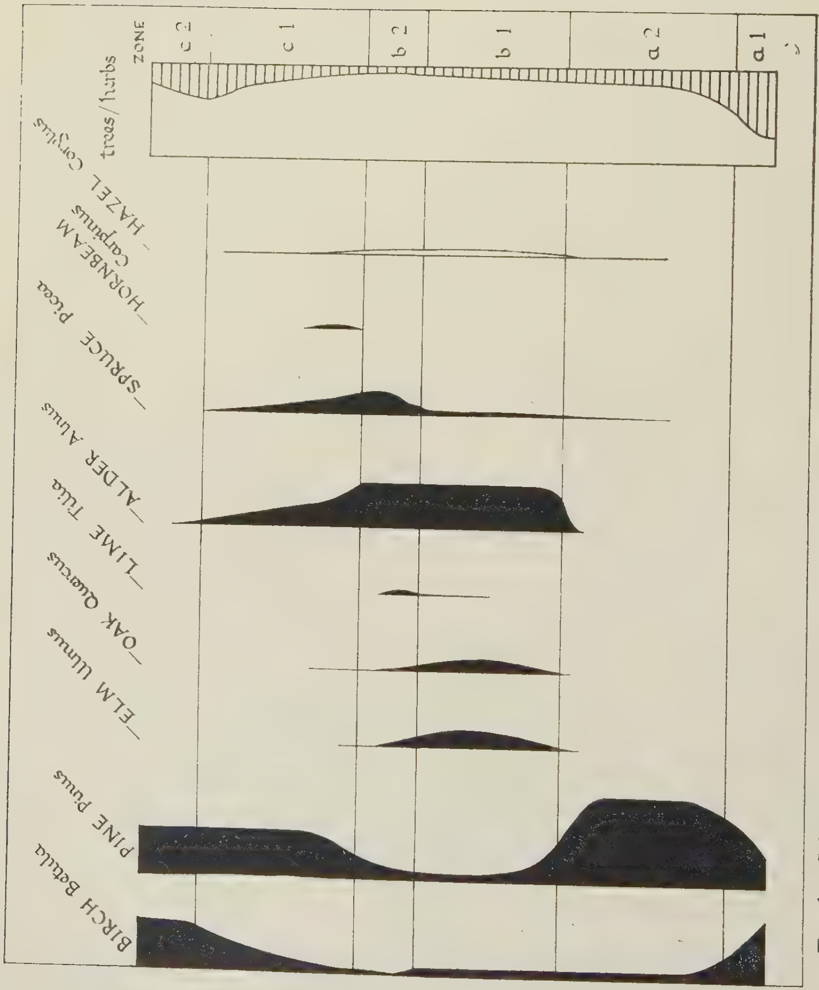

FIG. 1.—Schematic pollen diagram through the Cromerian Interglacial (Cromer Forest Bed), after Duigan.

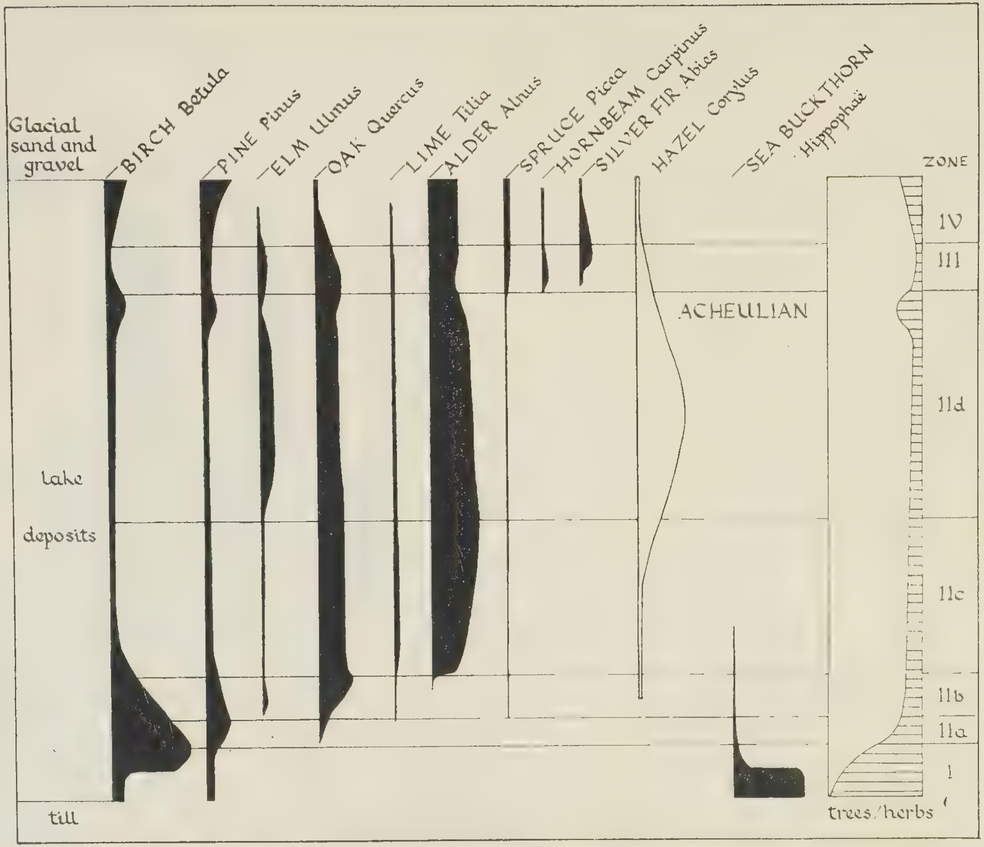

FIG. 2.—Schematic pollen diagram through the Hoxnian Interglacial (at Hoxne).

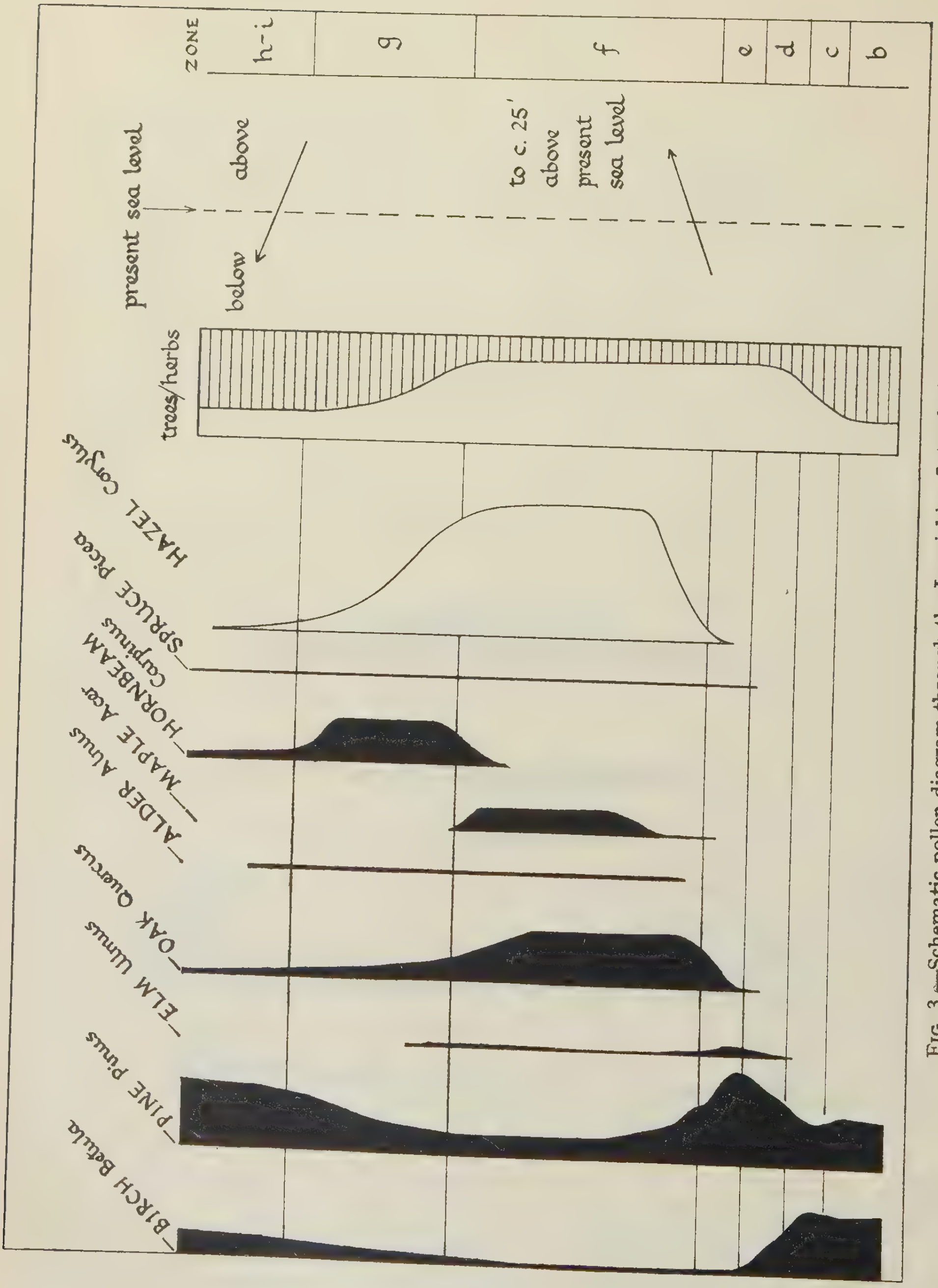

FIG. 3.—Schematic pollen diagram through the Ipswichian Interglacial (composite).

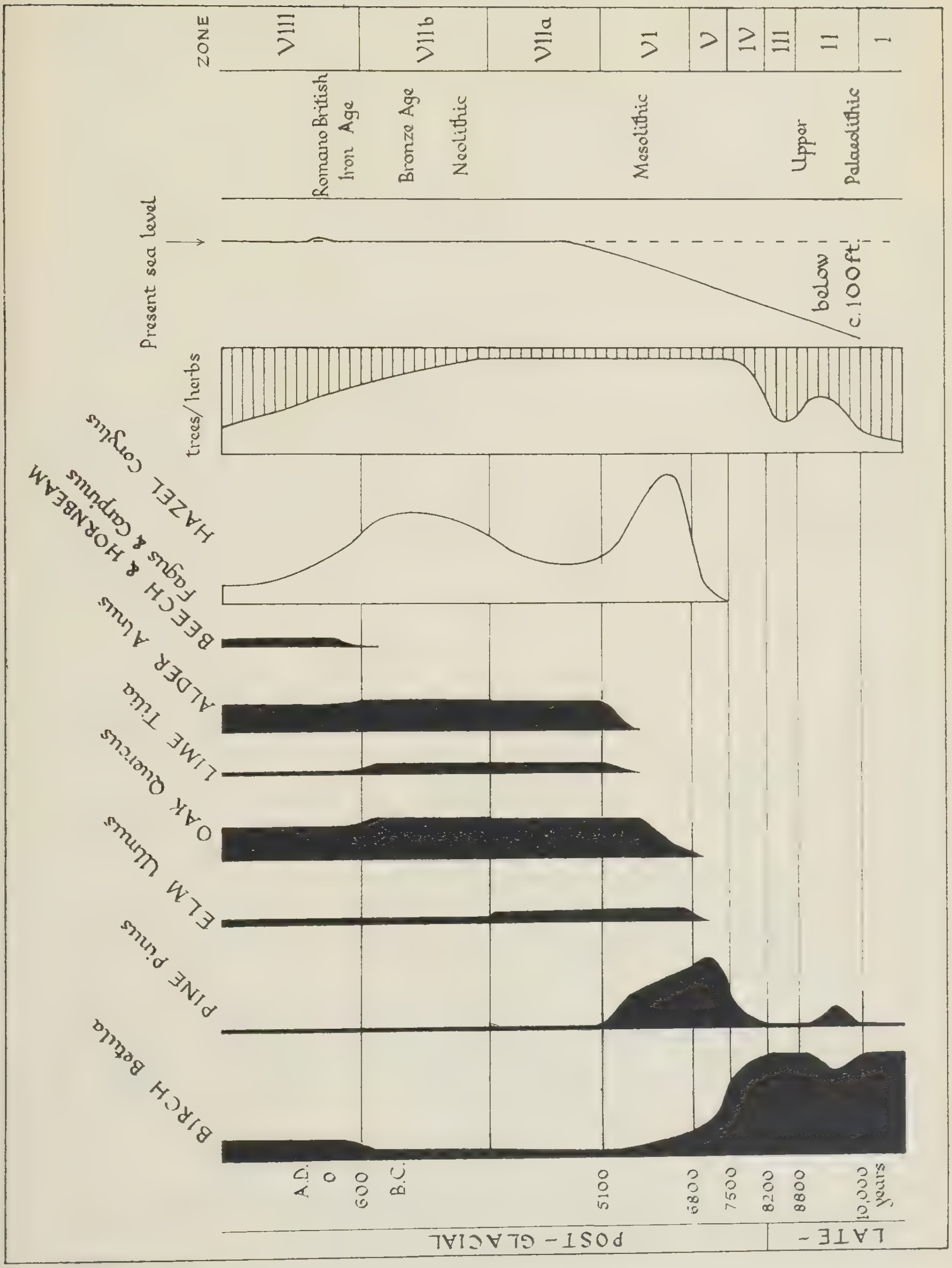

FIG. 4.—Schematic pollen diagram through the Late- and Post-glacial (composite).

tion, we may obtain some indication of the nature of the climatic change. Where species already present suddenly expand, this may give an indication of climatic change, e.g. the increase of *Tilia* pollen percentages at the Zone VI/VII transition in the Post-glacial is probably caused by an increase in warmth. Where the factors controlling the area of distribution of a species are known, then it may be possible to make more detailed deductions about climate from the fossil occurrence of such species. For example, Iversen's (1944) work on *Viscum, Hedera* and *Ilex* makes these genera valuable as climate indicators.

In comparing the climatic significance of vegetation types seen in the pollen diagrams we should remember that some plants may be excluded from immigration by barriers and also that we have to judge climatic indications from the present distribution and behaviour of the species. In respect of the present distribution, this is not necessarily determined by present climate and in respect of behaviour it is possible that ecological tolerances or some other property of the plant may have changed, but not the morphology of the part of the plant usually the fruit or seed, identified as fossil. It would be surprising if some selection of biotypes had not taken place in the many migrations enforced by the repeated climatic changes of the Quaternary.

As an example of climatic interpretation we may return to the Chelford Interstadial (Simpson & West, 1958). Here the pollen spectra were very similar to the pollen rain analyzed by Aario (1944) in the *Betula-Pinus-Picea* forest of northern Finland. Some approximation to the climate of the Chelford area during the deposition of the mud may be given by the climate of the area of distribution of this type of forest in northern Finland—annual rainfall 400–700 mm., annual temperature amplitude 20°–27° C., mean temperature of coldest month (February) $-10°$ to $-15°$ C., and that for the warmest month (July) 6° to 12° C.

The climatic differences between the interglacials are difficult to infer. For example, the Ipswichian Interglacial shows a very different pollen diagram from the other interglacials and from the Post-glacial, with high percentages of *Carpinus* pollen and much pollen of *Acer*, probably *A. monspessulanum*, fruits of which are found in the deposits concerned. Both these plants have a continental distribution and their abundance might be thought to indicate a climate more continental than that of the Post-glacial or of the Hoxnian Interglacial. In the latter, *Alnus*, *Hedera* and *Ilex* are all very well represented, perhaps an indication of a more oceanic climate than in the Ipswichian Interglacial where these plants are not common. But the differences between the Ipswichian and Hoxnian pollen diagrams might be due to accidents of distribution and the effect of barriers to migration. It will be seen that to disentangle the real climatic significance of the differences between the diagrams is very difficult.

I hope this gives you some idea of the interglacial and interstadial vegetation in this country. What is needed is more evidence of interglacial and interstadial vegetation from different parts of the country, and evidence of vegetation during the glaciations in parts of Europe which were refuges for the temperate flora. Only then will it be possible to give meaning to the differing vegetational successions we have seen in the non-glacial stages.

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Mr E. Oldfield made the following comments at the conclusion of the discussion of Dr West's paper :

In connection with the characterization of the Great Interglacial as a relatively ' oceanic ' episode, I should like to comment on findings from that period in the Biarritz area which may have some bearing on the question. Whereas the ' Atlantic ' plants mentioned by Dr Watt in connection with Irish deposits of that age were also present, (e.g. *Hymenophyllaceae*), there were also present in the Pays Basque at the time, a few types, (e.g. *Abies* sp.), which have more continental distributions at the present day. Since members of the *Hymenophyllaceae* are still abundant in the area now, and *Abies* for example does not reach the Pays Basque in its westernmost extent, one might be tempted to conclude that the climate of the time was not oceanic relative to the present day climate of the area, though it may have been so relative to the climate experienced there during any other Interglacial period. Evidence from France may also illuminate the problem of the times at which different species appear, in particular parts of Western Europe at the end of a glaciation. Whereas in the few dozen diagrams from Northern and Eastern France *Quercus* does not appear before *Corylus*, and in some cases definitely after *Corylus*, in the South-west, *Quercus* appears to have entered the area before *Corylus*. This may be a preliminary indication of the fact that some species of oak at least survived the glaciation in South-western Europe, perhaps in Iberia, whereas hazel was able to survive only in some refuge much further east. Although such a deduction is premature, it is founded on a great deal of evidence from French pollen diagrams and does suggest perhaps that the different times of migration of different species into an area after a glacial period are to some extent the reflection of different species surviving in different perglacial refugia.

SYMPOSIUM ON THE REPRODUCTIVE PHASE IN SEED PLANTS

HELD in the Society's Rooms on Friday, 8 January 1960 under the Chairmanship of Mr. A. W. EXELL, V.-Pres. L.S. and the Botanical Secretary.

1. WARDLAW, C. W.—Some preliminary observations on the inception of the inflorescence. page 90
2. CUTTER, E. G.—The inception and distribution of flowers in the Nymphaeaceae. page 93
3. HUDSON, J. P. & WILLIAMS, I. H.—Effects of environment and age on flowering in raspberries. page 101
4. HESLOP-HARRISON, J.—The experimental control of sexuality and inflorescence structure in *Zea mays* L. page 108
5. LONGMAN, K. A.—Factors affecting flower initiation in certain conifers. page 128

N.B.—The titles of the papers as now published do not correspond in detail with those on the published programme of the Symposium.

1. SOME PRELIMINARY OBSERVATIONS ON THE INCEPTION OF THE INFLORESCENCE

By C. W. WARDLAW, F.L.S.

Botany Department, University of Manchester

THE reproductive phase in angiosperms affords much scope for new investigations, including those relating to morphogenesis. Our knowledge of the morphology of inflorescence and flower is, of course, already very considerable as a result of taxonomic studies ; and this important classical aspect continues to afford opportunities, the more so as it is now being extended in various directions by the introduction of experimental procedures. Here my purpose is to enquire what are the major aims of the student of morphogenesis in this field and what may he hope to achieve.

Intending investigators of the reproductive organs of flowering plants may understandably feel overwhelmed by their vast number (some 250,000 species) and seemingly endless diversity. Almost any one of the larger orders or families presents a fascinating but alarming range of possible materials for study. So we may well ask : What is our main intention and how, and where, do we make a beginning? The writer's reflections have led him to the view that one aim not only offers hope of substantial progress being made but has the merit of being of a simplifying and unifying character : that is, a search for the main principles which underlie the morphological and functional development of the inflorescence and flower. It is a reasonable expectation that when we have a clearer understanding of some of the basic factors controlling development, based on the study of selected favourable materials, much of the confusing morphological diversity will appear to be no more than variations on a theme. Zygomorphy, for example, has apparently evolved quite independently in many different orders of dicotyledons and monocotyledons, but the plane of the zygomorphy is usually that of the axis and the bract. This suggests that certain relationships during growth and morphogenesis are of very general occurrence. The nature of such relationships can sometimes be discovered by observation, experiment and physiological analysis, the very earliest stages of development often being of paramount importance. Other characteristic features of floral structure found in species of quite different systematic affinity, and exemplifying what Goebel and others have referred to as homologies of organization, may eventually prove to be governed by the same general laws of development.

Although inflorescences and flowers are often conspicuously different from the organs formed during the antecedent vegetative phase, there is good support for the classical view that they are homologous with them. This concept is in accord with contemporary genetical views, i.e. that in the ontogenetic development of a plant, a major part of the genotype determines and controls the main organogenic developments, particular genes, or groups of genes, being also involved in particular characteristic developments. In some families, e.g. Ranunculaceae, these homologies of vegetative and floral organs are demonstrably present and closer analysis of floral morphogenesis in other groups may well show that homologies also exist where they are not immediately evident. In this connection, the heteroblastic development which is such a marked feature of the vegetative phase in some species often has its counterpart in the inflorescence, and may similarly lend itself to experimental treatment. For example, the writer has found that if the outer inflorescence bracts in *Petasites hybridus* (the butterbur) are removed, the inner bracts may develop a small lamina and resemble small foliage leaves. To sum up, it seems probable that closely comparable processes of growth and morphogenesis are involved in both the vegetative and reproductive phases though the final morphological developments may be so different.

In investigations of causality, it is important to consider the inception of the inflorescence with regard to the morphological organization of the plant, its ontogeny, and its seasonal development. In the somewhat unusual instances where a flower or inflorescence primordium originates in a leaf site, a consideration of the very fundamental but enigmatic problem of the inception of a patternized distribution of metabolites in the apical meristem becomes inescapable. The time of inception of the inflorescence during ontogenesis may often have important practical aspects, e.g. in the application of fertilizers and other cultural treatments. The banana, for example, with its complex inflorescence, the female part of which becomes the bunch of commerce, has its potential size, in terms of number of hands or clusters, definitively determined soon after the transformation of the vegetative apex ; i.e. the factors determining bunch size must effect their control at this early stage. Again, in palms, we tend to associate the large and showy male and female inflorescences with the adult stage. In some species, indeed, the plant is killed by the act of flowering and fruiting. In the oil palm (*Elaeis guineensis*), however, the writer has observed that, in precocious lines of breeding, bud primordia, which are the rudiments of inflorescences, may be present in the axil of the ninth or tenth seedling leaf.

For an experimental programme on inflorescence and floral morphogenesis, involving direct observations of the effects of treatments on the apex, it is essential to choose plants which can be readily dissected and examined at intervals under a binocular microscope, and which remain alive and continue to develop after experimental treatment. In general, this means using rosette plants or plants in which the inflorescence primordium is formed on a more or less substantial rhizome. Indeed, the search for favourable materials for observation and experiment may itself be indicated as an engaging task.

The time or season of inception of the inflorescence in perennial plants affords abundant scope for new observations. Although some investigations, chiefly relating to economic plants such as fruit trees, have been published, not enough is known of this aspect of the biology of flowering plants. Considerable variation in the time of inception, and also of development, of the inflorescence exists. In November, for example, the large rosette plants of *Digitalis purpurea* are still in the vegetative state ; and so also are several species of Umbelliferae. But species of *Viola, Dicentra* and *Arum* and many others have their floral development well advanced by autumn. The relationships between these developments and factors such as day-length, temperature, etc., require further investigation.

Some of the general points made above may be illustrated by referring to the common coltsfoot (*Tussilago farfara*), the apex of which has yielded observations of some considerable interest. The onset of the reproductive phase of development in this plant begins in early autumn, about September, as, indeed, Grainger noted in 1939. As in most flowering plants, the vegetative apical meristem changes considerably in size and form and gives rise to bracts instead of foliage leaves. Subsequently the primordia of the ray florets are formed acropetally on the inflorescence apex, the centre of which is still bare at this stage. Later still the primordia of the disc florets are formed in the central region of the inflorescence apex. At first these are approximately the same size as the ray floret primordia, but they very rapidly outgrow these, Pl. 1, Figs 1 and 2, although they were formed later. The growth pattern in this inflorescence thus undergoes important changes during development, the later-formed, more distal florets surpassing the earlier-formed peripheral ones in size. The difference in size can be well seen in a comparison of adjacent primordia of ray and disc florets, and persists during the subsequent development of the inflorescence. An interesting parallel phenomenon can be seen in the compound inflorescence of the related *Petasites hybridus*, in which the terminal capitulum is appreciably larger than the lateral capitula, although their formation is essentially acropetal.

These observations, fascinating as they are, do little more than raise problems. The important point is that these problems now seem open both to new systems of observation and analysis and to experimental investigation. For example, what causes the central florets to grow more rapidly than the earlier-formed peripheral ones? To what extent is this related to their ultimate structure, the ray florets being ‘ female ’, the disc florets functionally ‘ male ’? Can regions of the inflorescence apex originally destined to produce disc florets be caused to give rise to ray florets, and *vice versa*? What factors control the asymmetric development of the corolla in the ray florets, and to what extent is this linked with their other morphological attributes? These and many other problems relating to the inception of the inflorescence offer much scope for investigation.

The writer is indebted to Dr E. G. Cutter for kindly assisting in the preparation of this paper and presenting it on his behalf. Thanks are also due to Miss A. Walton and Mr G. Barker for technical assistance.

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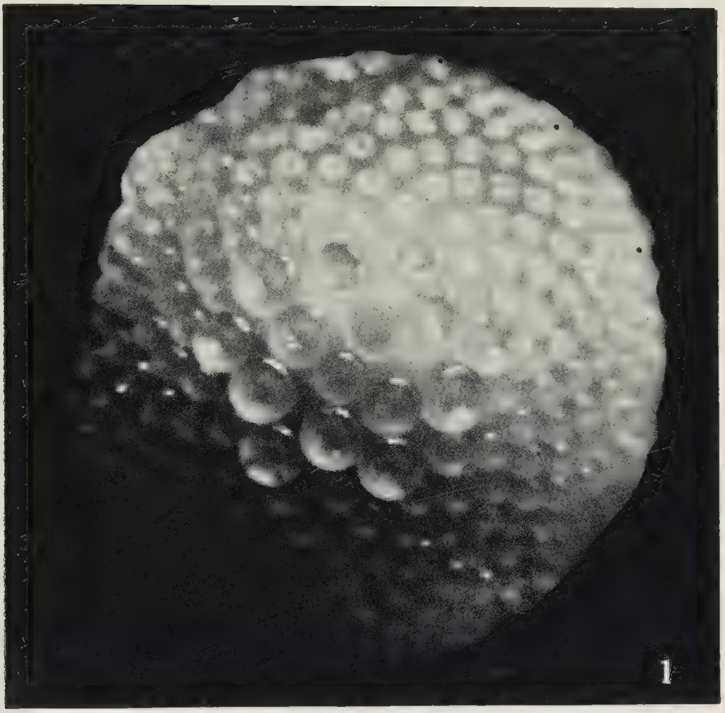
PLATE 1.

(*Photographs by G. Barker*)

FIG. 1.—*Tussilago farfara :* late autumn condition of capitulum, showing enlarged termina disc florets, as seen in surface view on dissection under a binocular microscope. (×40.)

FIG. 2.—*Tussilago farfara :* l.s. capitulum as shown above. (×50.)



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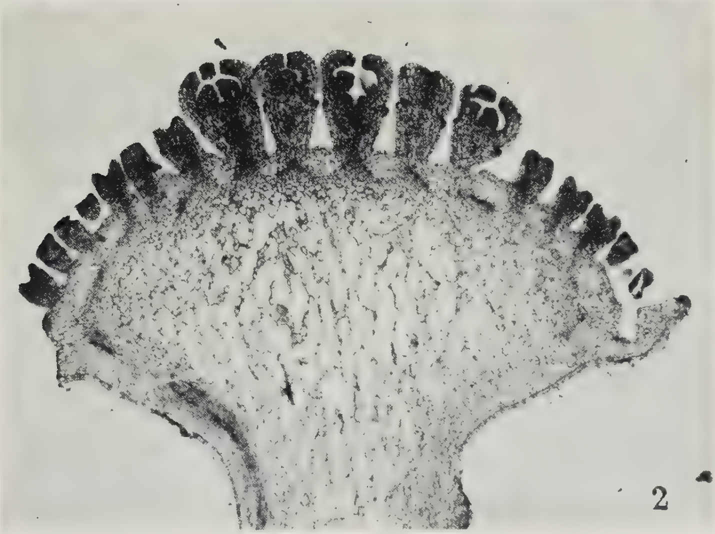

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2. THE INCEPTION AND DISTRIBUTION OF FLOWERS IN THE NYMPHAEACEAE

By Elizabeth G. Cutter

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In most of the angiosperms that have been examined, the flowering stimulus leads to the conversion of the terminal shoot apex or axillary buds to flowers or inflorescences. As a result of the onset of the reproductive phase, conspicuous, often irreversible, modifications in the growth pattern ensue, further vegetative growth being often due to the activity of a lateral bud. The present paper deals with the inception and arrangement of flowers in some members of the Nymphaeaceae, in which rather different changes, no less important, occur during the flowering phase. These observations raise problems of morphogenesis and developmental physiology which are worthy of consideration, even though no solution may yet be in sight. In the genera studied, flowers are formed on the apical meristem itself; they do not originate from detached meristems, and there is no preceding vegetative phase in their ontogeny. The rhizome apex continues to produce foliage leaves throughout its life, but after the onset of flowering it gives rise also to flowers: the growth of the apical meristem itself, however, remains indeterminate.

Materials and Methods

Of the eight genera comprising the family Nymphaeaceae (*sensu lato*), four will be considered. These four genera—*Nuphar*, *Nymphaea*, *Victoria* and *Euryale*—constitute the Nymphaeaceae (*sensu stricto*) and Euryalaceae of Li (1955). Rhizomes of *Nuphar* spp. and of *Nymphaea alba* L. were collected from natural habitats. Living material of *Euryale ferox* Salisb. and of *Victoria cruziana* d'Orbigny[1] and *V. trickeri* was obtained from British botanic gardens, and pickled rhizomes of *V. amazonica* (Pöppig) Sowerby (*V. regia* Lindl.) were obtained from the same source and from British Guiana. Through the kindness of these various donors, I have been able to examine six plants of *Euryale* and twelve of *Victoria* spp., in various stages of development.

The rhizomes of these genera were examined externally, after removal of the adventitious roots present below the leaf bases, and the sequence of organs noted. Expanded and unexpanded leaves and flowers were then progressively removed until the rhizome apex and surrounding primordia were laid bare, camera lucida drawings being made at intervals during the dissection. Finally the apical region was fixed, usually in chromacetic acid, sectioned longitudinally or transversely, and stained in Delafield's haematoxylin and safranin.

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[1] *Nomenclature.* In the available literature there is disagreement about the number of species of *Victoria* that should be recognized. Some authors (Li, 1955; Planchon, 1850-52, 1853) consider that there are at least two, and possibly three, species; others (e.g. Lemaire, 1847) hold that there is only one (*V. regia* (*V. amazonica*)) and that the others are merely varieties. *V. trickeri* is sometimes considered as a variety of *V. cruziana*, under the name *V. cruziana* var. *Trickeri* Tricker (Henkel, Rehnelt & Dittmann, 1907); and Hooker (1847) held that the *V. cruziana* of d'Orbigny (1840) was itself only a variety of *V. regia* (*amazonica*). In the absence of a modern monograph on *Victoria*, the material has been described here by the three specific names, as it was received; however, for the present purpose there is no essential morphological difference between them.

OBSERVATIONS

(i) *Nuphar* and *Nymphaea*

In *Nymphaea*, the flowers have no subtending bract and occur in leaf sites in the genetic spiral. This phenomenon, which has long been known, can be readily observed either by an examination of the mature rhizome or of the young primordia at the shoot apex (see Cutter, 1957 a, where earlier literature is cited). In *Nuphar*, peduncle scars again occur in the leaf parastichies on the surface of the rhizome, but a scale-like ' bract ' about 1 cm. long is present at the base of the mature peduncle. Consequently the flowers were formerly considered to be axillary. However, a study of early stages of floral development in four species of *Nuphar* has shown that this ' bract ' is the first-formed organ of the floral meristem, homologous with the first sepal of *Nymphaea* ; during growth the bract becomes progressively further removed from the floral meristem until it comes to be situated at the base of the peduncle (Cutter, 1957 b, 1959). Thus the flowers of *Nuphar*, like those of *Nymphaea*, occupy leaf positions in the genetic spiral. The rhizome apex in both genera produces a sequence of spirally arranged primordia, some of which develop as leaves and some as flowers. Very occasionally vegetative buds are also formed ; in *Nymphaea* they too occupy leaf positions and have no axillant leaf, but in *Nuphar* they are axillary (Fig. 1*a*, *b*).

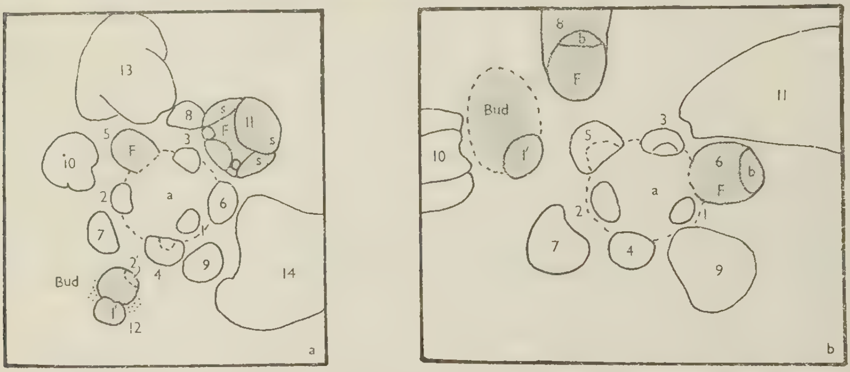

FIG. 1.—Surface views of rhizome apices with spirally arranged young primordia, numbered in order of increasing age :—

(a) *Nymphaea alba*. Apex of a specimen in which P_5 and P_{11} are flowers, and P_{12} is a vegetative bud with its first two leaf primordia. Hairs are present round the vegetative bud.

(b) *Nuphar lutea*. A specimen in which P_6 and P_8 are flowers, and P_{10} subtends a vegetative axillary bud with its first leaf primordium.

(*a*, shoot apex ; *b*, bract primordium ; *F*, flower ; *s*, sepal. The approximate extent of the apical meristem is outlined with a broken line ; flowers and vegetative buds stippled.) ×22.

The sequence of organs formed by the rhizome apex is of considerable interest. As Raciborski (1894 a) showed, the sequence of leaves and flowers differs in different species of *Nymphaea*. It seems likely, therefore, that the sequence of organs is affected by genetic factors, but since there is some variation in the sequence within any one species, as a study of *Nymphaea alba* and *Nuphar lutea* (L.) Sm. shows, other factors may also be involved. By statistical means, it can be shown that if a flower is present in *Nymphaea alba* at a node arbitrarily numbered 0, the probability of flower formation is much greater at successive even-numbered nodes than at intervening ones. There is an alternation between stimulation and inhibition of flowering in successive positions (Dormer & Cutter, 1959).

In *Nymphaea alba* there is some indication that vegetative buds occur in positions in the sequence of organs where flowers might have been expected. For example, on one rhizome of *N. alba* where an unusually large number of vegetative buds was present, the sequence of organs (Table I) indicates that these buds were formed two nodes after a flower, where on the basis of the findings of Dormer & Cutter (1959) another flower might have been expected.

TABLE I.—Sequence of organs on part of a rhizome of *Nymphaea alba* (arbitrarily numbered acropetally)

(○, flower ; □, vegetative bud ; otherwise leaves)

0	①	2	$\boxed{3}$	4	5	6	7	8	9	⑩	11	⑫
13	$\boxed{14}$	15	16	17	18	19	⑳	21	$\boxed{22}$	23	24	25
26	27	28	29	30	㉛	32	$\boxed{33}$	34	35	36	37	38
39	㊵	41	$\boxed{42}$	43	44	45	46	47	48	㊾	50	(51)
52	(53)	54	$\boxed{55}$	56	57	58	59	..	..	..	..	..

(ii) *Victoria* and *Euryale*

On the vertical rhizomes or rootstocks of mature plants of *Victoria* and *Euryale* leaf bases can be readily distinguished from those of peduncles by the associated adventitious roots and by the pattern of the major air canals : in peduncles the four main air canals are of equal size, in the petioles the two adaxial air canals are larger. Thus distinguished, five leaf parastichies can be observed encircling the rhizome in one direction, with five parastichies of flowers intervening between them ; passing in the other direction are eight parastichies—usually less distinct—in which flower and leaf bases alternate (Pl. 1, fig. 1). In other words, during the flowering phase there are two homodromous spirals, one of leaves and the other of flowers (Pl. 1, fig. 2). These facts have long been known (Henfrey, 1852 ; Planchon, 1850–51 ; Raciborski, 1894 a, b ; Schumann, 1890, 1894 ; Seidel, 1869), but their morphogenetic significance has not been adequately considered.

When successive flowers and leaves, and their enveloping stipules, are removed, the young leaf and flower primordia at the rhizome apex are eventually revealed. These occupy very precise positions with respect to one another and can be seen to be arranged in two spirals (Fig. 2a, b). A flower occupies a position at one side of the axil of an older leaf, and also has a younger leaf primordium adaxial and just lateral to it. In all the specimens of *Victoria* and *Euryale* which I have examined the flower is situated towards the anodic side of the older leaf. The only exception to this which I have found is a published drawing of an apex of *E. ferox* (Raciborski, 1894 a, fig. 9), in which the flowers are apparently situated at the cathodic side of the leaf axil. This relationship is in any case a little less obvious in *Euryale*, where at least in some specimens the flowers seem to be rather closer to the centre of the leaf axil, than it is in *Victoria* (Fig. 2 ; Pl. 2, figs 1 and 2). These observations alone cannot decide whether the flowers should be interpreted as non-median axillary structures, or extra-axillary organs. Theoretical aspects of this matter were discussed by Raciborski (1894 a, b) and Schumann (1890, 1894). Henfrey (1852) took the view that the flowers were axillary. Seidel (1869) considered that the flower was correlated with the older leaf abaxial to it, because it was surrounded in the bud by the stipule of this leaf. However, this is probably a consequence of the fact that the flower and the stipule of this leaf are formed at about the same time, usually when the leaf is at about P_3 (Fig. 2*b*). Whether or not the flowers can be homologized with other organs, it is important to achieve both an accurate description and an adequate explanation of the inception of the various organs at the apical meristem.

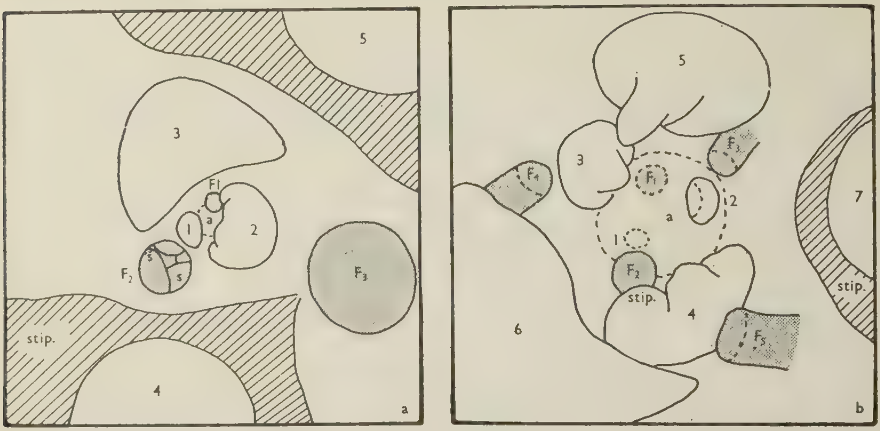

FIG. 2.—Surface views of rhizome apices with young leaf and flower primordia. The flowers occupy sites to the anodic side of the axil of an older leaf; they also have a younger leaf primordium adaxial to them :—

(a) *Euryale ferox*. Apex of a young plant in which the first three flowers (F_3–F_1) have been formed.

(b) *Victoria amazonica*. Apex of a mature specimen from British Guiana. The peduncles of the older flower primordia are bent over a little towards the rhizome apex.

(*a*, shoot apex; *F*, flower; *stip.*, excised stipules. Stipules cross-hatched, flowers stippled.) ×22.

As Seidel (1869) pointed out, the period of development (i.e. expansion) of leaf and flower in *Victoria* must be the same; it is clear that the plastochrone

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EXPLANATION OF PLATES

PLATE 1

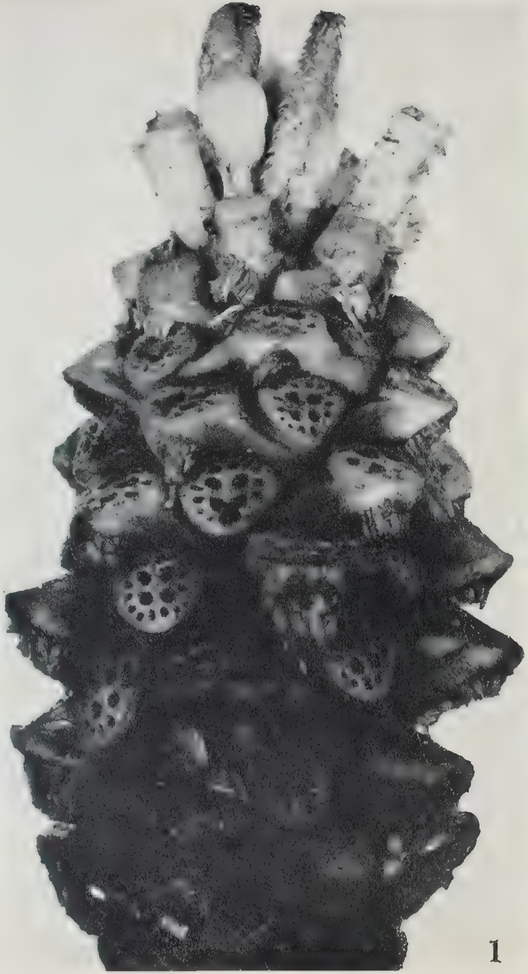
FIG. 1.—Side view of a 10-month-old rhizome of *Victoria trickeri*, showing separate leaf and flower parastichies passing to the right. Roots and the outermost stipules have been removed. Leaf bases have associated adventitious roots; peduncle bases have no associated roots and show four central air canals of equal size. Young, unexpanded leaves and flowers are present at the tip of the rhizome. $\times\frac{1}{2}$.

FIG. 2.—View from above of the tip of the same rhizome, after the removal of the outer leaves, flowers and stipules. The bases of excised petioles and peduncles can be seen: peduncles have four main air canals of equal size, petioles have four main canals of which the two adaxial ones are larger. In the centre, young unexpanded leaves and flowers can be seen. Separate spirals of leaves and flowers can be discerned, passing anticlockwise from younger to older organs. The severed bases of the stipules can be seen between these organs. ×2.

PLATE 2

FIG. 1.—Transverse section of the apex of a young plant of *Euryale ferox* in which the first two flowers (F) had been formed. These occupy positions anodic to the axil of an older leaf. ×22.

FIG. 2.—Transverse section of the apex of the specimen of *Victoria trickeri* illustrated in Fig. 3, showing the relative positions of leaves and flowers and the absence of f_9 from the floral spiral. *See* Fig. 3 b for numbering, etc. ×22.



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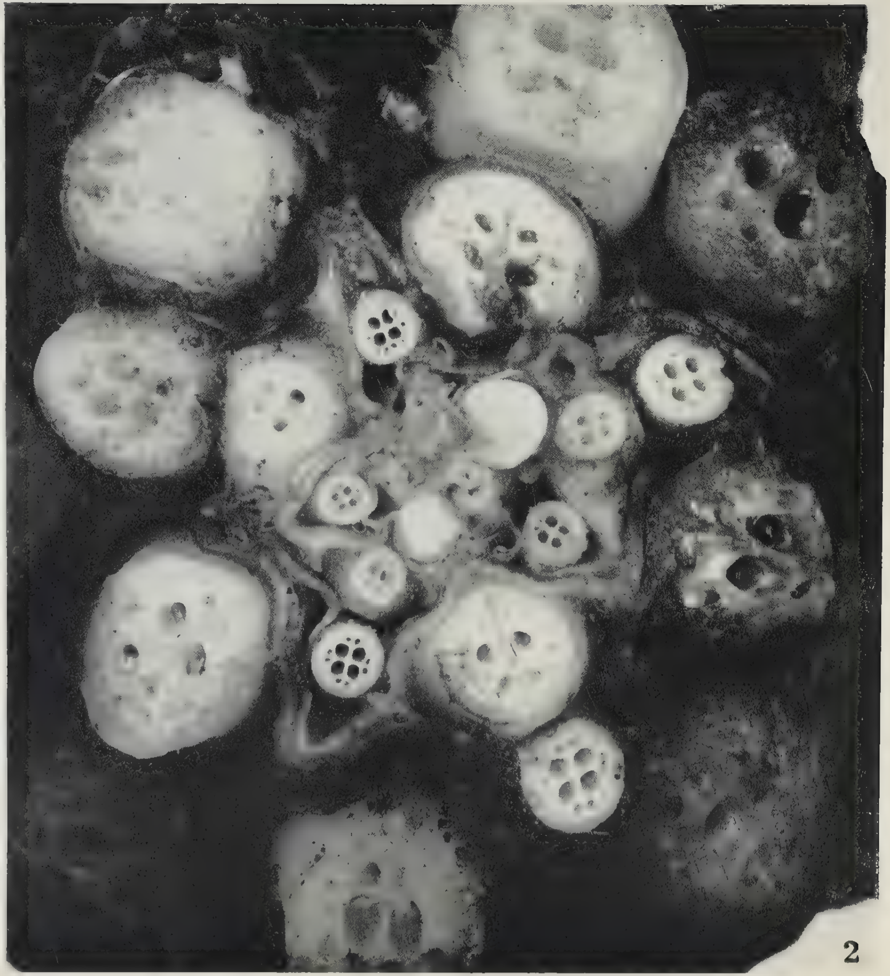

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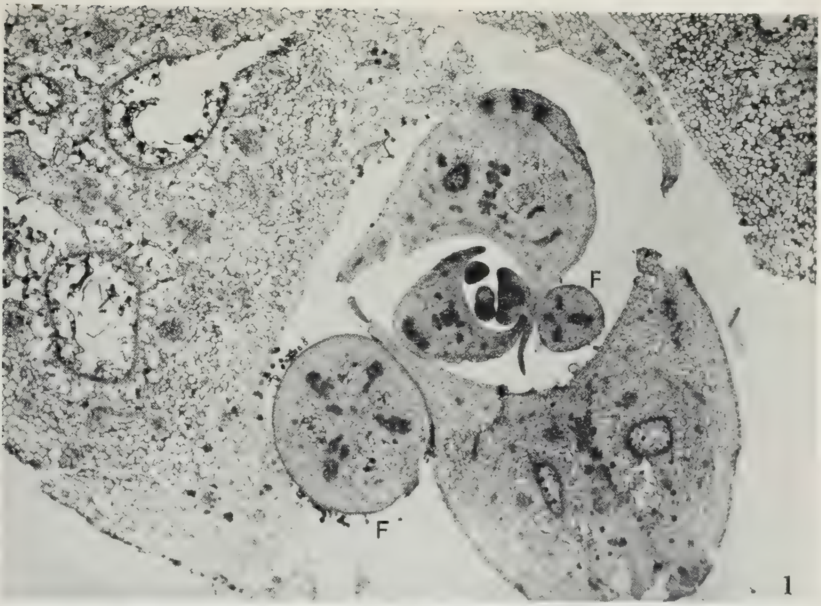

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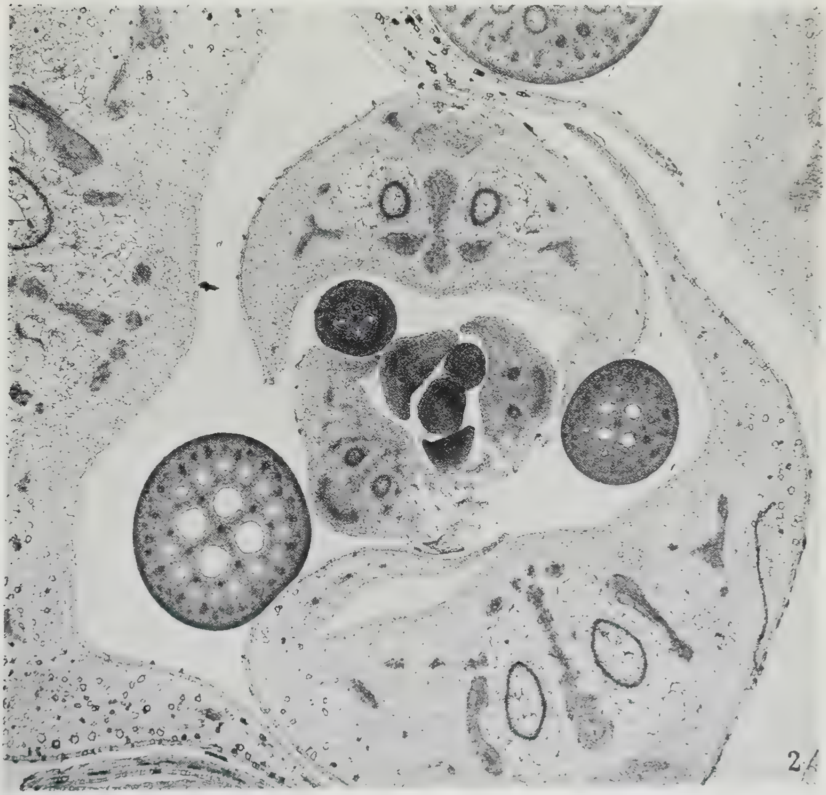

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must also be of the same duration. Both spatial and temporal relationships between leaf and flower primordia are, in fact, of considerable interest. In apices of *Victoria* and *Euryale* a flower primordium is formed just before the leaf primordium which is almost adaxial to it (Fig. 2*b*, where F_2 has P_1 adaxial to it, but no primordium is yet visible adaxial to F_1). P_1 and F_1 are formed almost, but not quite, simultaneously in different sectors of the apex, and two primordia of diverse morphological destiny, F_2 and P_1, are formed in rapid succession in close proximity. The sequence of organogenesis is thus P_2, F_2, P_1, F_1 and so on.

In young plants of both *Victoria* and *Euryale* which had been grown in Britain the first flower was formed after about 14–16 leaves, as far as could be judged from the leaf scars. In mature specimens of *V. amazonica* from British Guiana the base of the piece of rhizome received was sometimes devoid of flowers, indicating either that under those conditions flowering began later in the ontogeny of the plant or that it was seasonal.

The spiral of flowers in *Victoria* is usually described as continuous from its inception, and at least in one-year-old plants grown in Britain this is usually so. However, certain exceptions of considerable interest were observed. In a young plant of *V. cruziana* which had just begun to form flowers, the first flower was present, then the second was missing from the appropriate position, but the spiral was thereafter continuous as far as development had gone. Another young plant of *V. cruziana* was received from the Royal Botanic Garden, Edinburgh, and subsequently grown on for a short time under rather unfavourable conditions in Manchester. On dissection of this plant it was found that the first three flowers were succeeded by a phase of purely vegetative growth. In a fairly small specimen of *V. amazonica* from British Guiana the flower spiral was also not continuous (Table II). The leaves were arbitrarily numbered acropetally, and for the purpose of the table a flower is considered to be associated with that leaf to the axil of which it is anodic.

TABLE II.—Flowering in a specimen of *Victoria amazonica* from British Guiana

(○, flower present in position described in text ; otherwise leaf solitary)

⓪	①	②	③	④	⑤	⑥	7	8	⑨
10	⑪	12	13	⑭	⑮	⑯	⑰	⑱	⑲
⑳	21	22	23	24	25	26	27	28	29
30	31	32	33	34	..	..	..	..	..

In two specimens of *V. trickeri* which were eight months old when examined, but which had never attained any great size, flowering was also discontinuous. In the larger of the two specimens, three flowers (numbered acropetally) were formed (f_1–f_3), f_4 was missing, f_5–f_8 were present, f_9 was missing, and f_{10} was present (Fig. 3*a*, *b* ; Pl. 2, fig. 2). In the smaller specimen, two flowers (f_1 and f_2) were formed, f_3 and f_4 were missing, and f_5–f_8 were present. Notwithstanding the absence of the intervening flowers, younger flowers were precisely in the normal positions with respect to the leaf primordia.

Vegetative buds have never been observed in either *Victoria* or *Euryale*, and no reference to them has been found in the literature.

DISCUSSION

In these four genera of the Nymphaeaceae, the inception and distribution of flowers are rather unusual. In *Nymphaea* and *Nuphar* the rhizome apex, or sectors of it, apparently must alternate between different physiological states : that promoting flower, and that promoting leaf, formation. During both the vegetative and flowering phases in these genera there is a single genetic spiral; the stimulus to flower inception evidently coincides, or is in phase with, that which leads to the formation of growth centres during the vegetative phase, and in consequence flowers occupy leaf sites. In *Victoria* and *Euryale*, by contrast, the stimulus to flower formation is of the same frequency as, but out of phase with, that leading to leaf formation, and two genetic spirals result.

In *Nymphaea* and *Nuphar* there is some evidence that vegetative buds are produced in positions where flowers would have been expected, i.e. that some of the factors necessary for their inception correspond to those necessary for flower formation. In *Victoria* and *Euryale* no such relationship apparently exists : if the conditions required for flower inception are not wholly fulfilled no organ is formed in that position.

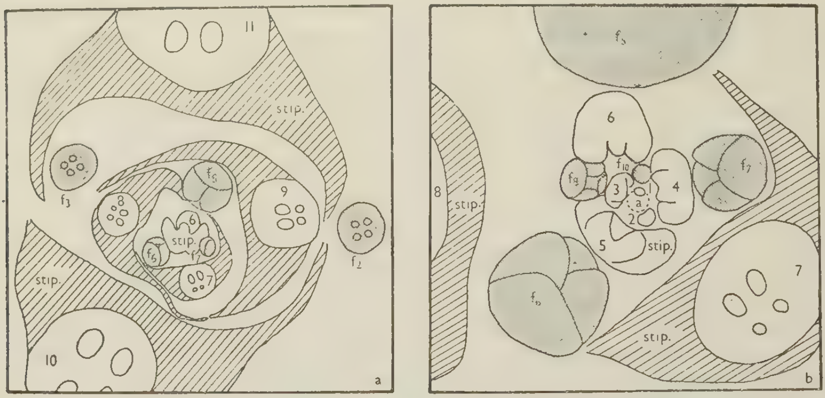

FIG. 3.—Surface views of a specimen of *Victoria trickeri* at stages during dissection. Flowers occupy sites to the anodic side of the axil of an older leaf. The leaf spiral is continuous, but occasional organs are missing from the floral spiral.

(a) The severed peduncles of the second and third flowers to be formed (f_2 and f_3) are shown (f_1 was out of view) ; f_4 is missing from the spiral, and f_5–f_7 are present. Younger leaves and flowers are concealed within the stipule of P_6. (×2¼.)

(b) Apex of the same specimen, after the removal of further stipules. f_8 continues the floral spiral, f_9 is missing, and f_{10} is again present. See also Pl. 2, fig. 2. (×9½.)

(*a*, shoot apex ; f_2–f_{10}, flowers (stippled) numbered in order of formation ; *stip.*, stipules (cross-hatched when excised) ; 1–11, leaf primordia numbered in order of increasing age).

It is important to consider the whole pattern of organogenesis at the apex. Prior to the visible appearance of the complex pattern of primordia, there must be a patternized distribution of metabolites, including some that may be essential for the formation of particular organs ; the ultimate problem is to reach an understanding of how these patterns are initiated. In *Nuphar* and *Nymphaea* it is clear that all the organs are components of a single pattern ; in *Victoria* and *Euryale* the presence of separate spirals of leaves and flowers might suggest that these constituted autonomous patterns. However, the observation that in *Victoria* flowers can apparently be omitted from the spiral without affecting the position of consecutive flowers lends support to the view that the positions of flowers are closely correlated with those of the leaves, and suggests that in these genera also the whole pattern should be considered as a single entity. Raciborski (1894 b), indeed, considered that the sites of flower formation were determined by those of older leaves.

In this connection, it is of considerable interest that Snow & Snow (1942) have shown that in some species, at least, some stimulus from the young leaf primordium is necessary for the formation of the (vegetative) bud in its axil. At the last of these symposia, Audus (1959) suggested that a system in which the various components of a complex necessary for bud formation were derived from the leaf primordia, the apical dome and perhaps also the developing axis, could supply the mechanism both for the inception and positioning of the lateral bud. The observations described in the present paper suggest that a physiological situation of remarkable complexity must exist in the rhizome apices of these members of the Nymphaeaceae. In all four genera, the inception of leaf and flower primordia alternates, at least to some extent; but whereas in *Nuphar* and *Nymphaea* flowers occupy sites in the existing foliar spiral, in *Victoria* and *Euryale* they form a separate spiral from that of the leaves. The proportion of flowers formed relative to leaves differs in the various genera, as do the resulting patterns of organs. However, the prevalence of the alternation of leaf and flower suggests that the underlying mechanisms involved in the formation of the various patterns may ultimately prove to be not so very different. It seems clear that investigations both of cell physiology and of how substances affecting growth become distributed in the apical meristem are required. Techniques of sufficient delicacy to investigate the biochemistry of the apical region, however, are not yet available. Histochemical studies of the kind already successfully carried out by Van Fleet (1959 a, b) might well prove valuable.

It is possible to think of various ways of investigating some of the problems described above by experimental means; but the difficulties of the materials, especially *Victoria*—notably its size, its rarity, and its aquatic habitat—are considerable. Some of the possible relationships between individual leaves and flowers might be investigated by surgical experiments on young primordia, similar to those of Snow & Snow (1942), and perhaps also by photoperiodic treatments of certain leaves, or by nutritional experiments. Experience with *Nuphar* and *Nymphaea*, however, indicates that water-lilies are not ideal material for surgical experiments, or for continuous observation of growth at the apex. Nevertheless, some of the aspects of morphogenesis described here deserve further study, since they must be taken into consideration—whether or not they are ultimately found to be of more general occurrence—if a full understanding of the reproductive phase of seed plants is to be achieved.

SUMMARY

In *Nuphar* and *Nymphaea* flowers are formed in leaf sites in the genetic spiral. The sequence of flowers and leaves is to some extent characteristic of the species; in *Nymphaea alba* there is alternation between stimulation and inhibition of flower formation. Vegetative buds occur occasionally in positions where flowers would be expected. In *Victoria* and *Euryale* flowers are formed in a separate spiral from the leaves; flowers occupy precise positions which may be described as to the anodic side of the axil of an older leaf. Flowering in these genera is not necessarily continuous after its inception, but even where there are gaps in the flower spiral subsequent flowers occupy normal positions; flower sites may therefore be more closely related to those of the leaves than to those of other flowers. Vegetative buds have never been observed.

In all these genera, flower primordia are formed on the apical meristem, which itself continues indeterminate growth and gives rise to both flowers and leaves. Consequently physiological conditions in the rhizome apices must be exceedingly complex: in all these genera conditions favouring leaf and flower

inception must alternate in specific ways, leaves and flowers being sometimes formed very close together in both time and space.

Acknowledgments

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3. EFFECTS OF ENVIRONMENT AND AGE ON FLOWERING IN RASPBERRIES

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Introduction

The red raspberry (*Rubus idaeus* L.) is unusual amongst crop plants in that it bears a succession of short-lived woody shoots on a long-lived perennial stool and root system. Each shoot passes through a sequence of well-defined phases during the course of its life, which lasts for about two years, making the raspberry shoot an interesting subject for studying the effects of seasonal weather on growth, flower initiation, and dormancy.

Phases of Development and Growth

The phases of development and growth which normally occur in Britain can be described briefly as follows (Hudson, 1959) :—

Phase 1 : *Initiation of a root bud* (Fig. 1a).—Numerous adventitious buds arise naturally on raspberry roots (i.e. not only after injury of the root, as in some other species) and buds can be found at all times of the year, although they are only capable of elongating from about August to April (Hudson, 1954 and 1955).

Phase 2 : *Subterranean sucker* (Fig. 1b).—When root buds commence to grow a few of the proximal internodes elongate rapidly, carrying the growing point to the surface of the soil.

Phase 3 : *Emergent sucker* (Fig. 1c).—Where buds elongate in the late summer or autumn, extension growth ceases shortly after the tip emerges from the soil but a number of leaves expand, to produce a rosette near ground level. This emergent pause is less well-defined when suckers emerge above ground in the spring, and no rosette is formed (Williams, 1959 a and b).

Phase 4 : *First winter dormancy*.—Shoots which emerge before the onset of winter shed most of their leaves during the winter, and become dormant.

Phase 5 : *Elongating shoot* (Fig. 1d).—Shoots grow strongly during the period from spring to late summer attaining a height of several feet and becoming lignified. This is the main period of growth, in which the ' new cane ' of horticultural practice is produced. During this period branching rarely occurs and the shoot exhibits a marked apical dominance.

Phase 6 : *Cessation of vegetative growth and initiation of flower buds* (Fig. 1e).—Growth of the shoot slows down towards the end of the summer and a terminal cluster of leaves is produced as a result of the failure of the upper two or three internodes to elongate. Flowers are usually initiated in the terminal bud shortly after the shoot ceases to elongate, followed by the initiation of flowers in axillary buds situated a few nodes below the apex, initiation occurring later in other buds above and below until, by mid-winter, all axillary buds contain flower primordia except for a few towards the base of each shoot. Buds become increasingly complex as floral organs develop and more flowers are initiated, and this process continues until the spring. Once flower initiation has

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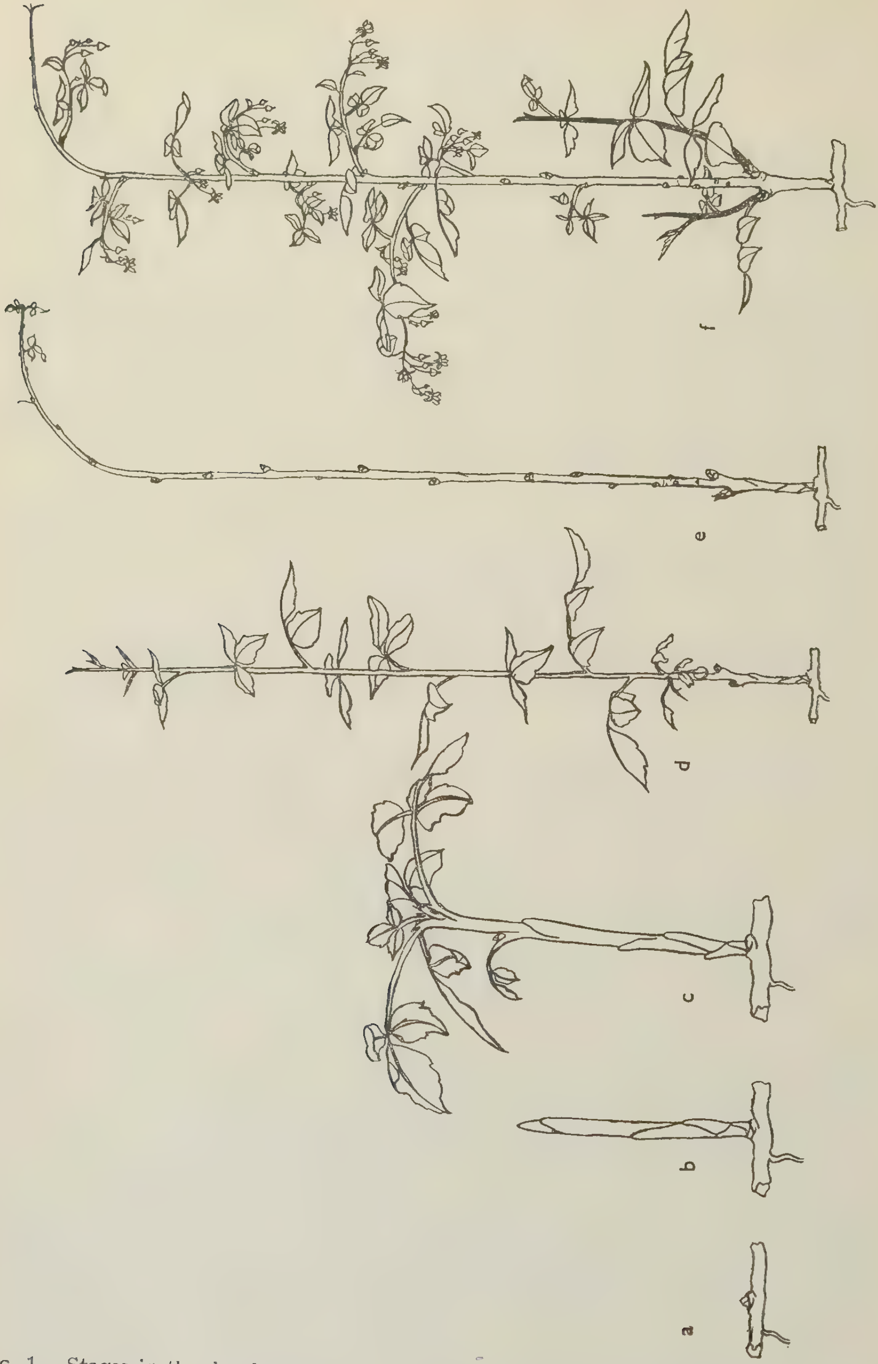

FIG. 1.—Stages in the development of a raspberry root sucker (separate drawings not to same scales). (a) Initiation of bud on root; (b) shoot elongating to the soil surface; (c) emergent root sucker with rosette of leaves just above soil level; (d) elongating shoot during summer; (e) condition of shoot in the autumn, with terminal cluster of small leaves and well-developed basal buds; (f) fruiting shoot, with two strong vegetative shoots growing from the basal buds.

occurred, the rate of subsequent development of the inflorescence is probably governed by climatic conditions, periods of low temperature retarding what would otherwise be a continuous process (Williams, 1959 c).

Anomalous Phase 6 : *Tip flowering.*—In some varieties (e.g. Lloyd George) flower initiation occurs in the terminal bud a few weeks earlier, whilst shoots are still elongating, in which case the flowers continue to develop to full maturity without a dormant phase, often resulting in a late crop of fruit in the autumn, after which the fruiting tip of each shoot dies.

Phase 7 : *Breaking dormancy of flower buds.*—In common with many other deciduous woody species, raspberry flower buds do not normally start to grow until the spring, even though there are mild spells of weather during the winter, suggesting that the buds require to experience a certain amount of cold before they can respond to higher temperatures. This is borne out by the fact that raspberry buds sometimes fail to grow out normally in the spring after exceptionally mild winters in Britain (Harris, 1940), or when attempts are made to grow raspberries in slightly warmer climates (e.g. in the more northerly parts of New Zealand).

Phase 8 : *Flowering and fruiting* (Fig. 1f).—Once dormancy has been broken by sufficient winter cold, buds commence to grow when weather conditions are suitable in the spring, producing laterals which bear both leaves and flowers.

At the same time one or more of the basal buds, near ground level, start to elongate vigorously, developing into a vegetative replacement shoot, which repeats the biennial cycle of phases 5–9.

Anomalous Phases 5–8 : *Flowering on new shoots.*—Occasionally, what would normally be a vegetative ' replacement shoot ' initiates flowers and produces fruiting laterals from most of its axillary buds in the season in which it grew from a basal bud, i.e. becomes, in effect, a large ' fruiting lateral ' instead of remaining vegetative. Such shoots die after fruiting and can thus be regarded as annual rather than biennial, a habit which is normal for some of the Rubus species that grow in lower latitudes.

Phase 9 : *Senescence and death.*—After fruiting, the whole shoot dies back to the position from which a replacement shoot has grown, the bases of successive shoots forming a long-lived perennial structure of increasing complexity.

Effects of Weather and Age

The morphology of a shoot depends on three factors, (a) whether the apical meristem is producing new leaf primordia, flower primordia, or no new primordia at all ; (b) whether the primordia expand or not and, if the former, on the rate of expansion ; (c) whether the internodes elongate or remain short and (d) whether axillary buds are initiated and, if so, whether they remain dormant or grow out into side branches. Raspberry shoots arising from root buds are of interest from an experimental point of view because of the various combinations in which these phenomena occur.

The three major phenomena of vegetative apices, namely leaf initiation, internode elongation and leaf expansion are each dominant, separately and in turn, in phases 1, 2 and 3 respectively. By contrast, all three phenomena occur concurrently in the elongating shoot in phase 5. Flower initiation occurs in buds and internodes cease to elongate in phase 6, while various conditions of " dormancy " can be studied in the vegetative apex (phase 4) and in fruit buds (phase 7).

The regularity with which the pattern of behaviour is associated with the changing seasons of a temperate climate might suggest that the passage from one phase to the next is entirely controlled by weather conditions. On the other hand, since the successive seasons are spaced apart in time, a temporal, or ageing, factor might also play a part in determining the differing behaviour patterns.

There are, in fact, three possibilities, all capable of experimental study :—

(a) If developmental behaviour is entirely in response to environment, then plants which have previously experienced different environmental conditions should behave in the same way if put into any particular new environment ; and it should be possible to hasten or delay the sequence of phases at will by moving plants through a succession of suitable environmental conditions, leading for instance, to the production of fruit on very young shoots or the maintenance of shoots in a particular phase for prolonged periods of time.

(b) If development is due primarily to the passage of time, or the effects of time-controlled endogenous rhythms within the plant, this fact would be manifest if plants of different past histories were grown together in a similar environment, since they would then be expected to behave differently.

(c) If progress through the various stages depends partly on internal factors (such as, for instance, the 'physiological age' of a shoot) and partly on the effects of environment, such a system of dual control could be demonstrated in two ways—if plants fail to pass from one phase to the next when put into an environment which normally favours the second phase, until after the lapse of a certain minimum of time (or after a minimum amount of growth) ; or if plants ultimately pass to the next phase under conditions in which that phase does not normally occur.

Experiments Under Controlled Conditions

To study these aspects a series of experiments was carried out with plants of Malling Promise raspberry in growth rooms where temperature, light intensity and daylength could be controlled (Hudson and Williams, 1957).

Emergent Suckers and Young Shoots

Young raspberry plants were subjected to various combinations of temperature (about 10, 15 and 21° C) and day-length (9 and 14 hrs), at a light intensity of about 450 foot candles. All plants at 21° C. continued to elongate, in both short and long days ; at 10° C. all plants ceased to elongate, and formed terminal rosettes of leaves, at both day-lengths ; while at 15° C. plants in long days continued to elongate whereas those in short days became rosetted.

The terminal buds of rosetted plants gradually became dormant. This process was reversible in the early stages, since shoots started to elongate again if given better growing conditions, but after a period of about ten weeks dormancy became complete. Terminal buds failed to grow when plants were then returned to higher temperatures and long days, but shoots grew vigorously from basal buds near ground level. However, dormancy of the terminal bud was readily broken by subjecting dormant plants to low temperature (3° C.) for a few weeks, after which those buds grew readily under suitable growing conditions.

These, and other, observations (described by Williams, 1959 b) show that the behaviour of young raspberry shoots is largely governed by the range of climatic conditions that occurs from late summer to early spring. Shortening days and falling temperatures in autumn bring about the onset of dormancy of young shoots which have emerged above ground. Dormancy is broken during winter by low temperature, and in the spring those shoots which have over-wintered respond to lengthening days and rising temperatures by growing vigorously.

In recent experiments, not yet completed, vigorously elongating young plants have been put under conditions of relatively low temperatures and short days and held there for long periods of time. As expected, all plants responded by ceasing to elongate and terminal rosettes were produced, but after many months the plants commenced to grow again, both terminal buds and basal buds producing strong shoots under environmental conditions that prevent younger shoots from growing at all.

Flower Initiation—Effect of Environment

Flower initiation in buds of plants at the 20-node stage was found to be closely correlated with temperature and day-length. At about 15° C. no flowers were initiated in long or short days. At 13° C. no buds became floriferous in 16 hour days but a few buds towards the apex of shoots had flower initials after six weeks when plants were given the same temperature in 9 hour days. At 10° C. flowers were initiated rapidly at both daylengths, but more quickly in the shorter days.

It seems that initiation of flowers in raspberry shoots does not normally occur in temperate climates until temperatures fall to relatively low levels (except in certain rare anomalous cases). Flower buds will then be formed, quickly if days are short but more slowly if they are still long (i.e. when cool weather occurs early in the autumn).

Breaking Dormancy

If plants with well-developed flower primordia in the buds are put into good growing conditions immediately after receiving the inductive treatment, the buds either fail to grow or do so erratically and only after a long delay. By subjecting plants to low temperatures of about 3° C., after flower buds have been initiated, the dormancy of these buds can be broken in about four weeks, after which they respond rapidly to warmer conditions and grow out into fruiting laterals. The last stage seems to be little affected by day-length provided there is sufficient light for healthy growth.

One of the most interesting results from the whole series of experiments was shown by plants which were left in a dark room at 3° C. for nearly a year, at the end of which time they started to grow strongly and produced long etiolated shoots before finally dying, under conditions which usually appeared to maintain complete dormancy of shoots.

Flower Initiation—Effect of Age (Fig. 2)

Mature shoots cease to elongate in the autumn and produce a terminal cluster of leaves. This response, rather similar to that of young shoots a few centimetres high, appears to be induced by shortening days and falling temperatures of the autumn, but flower primordia are initiated in buds of mature shoots whereas those of young shoots remain vegetative. Thus some sort of " ageing " process appears to be involved, and this has been studied by subjecting plants of different sizes to conditions that were known to lead to induction of flowers in buds on mature shoots (Williams, 1960).

Flowers were not initiated in buds, even under the most favourable inductive treatments, in plants that were 5 or 10 internodes long. Plants with 15 internodes were able to produce a few flowering laterals, but only after prolonged inductive treatment. Plants with 20 nodes developed flower buds readily when given inductive treatment for as little as two weeks, with an increase in the number of flower buds as the treatment was extended to five weeks.

Rather unexpectedly, plants which were 30 nodes long proved not to require inductive treatment at all. A period of six weeks at a temperature of about 4° C. not only caused flowers to be initiated, but also broke the dormancy of the flower buds.

Thus induction of flower buds appears to become less dependent on particular climatic conditions as shoots become older and more mature.

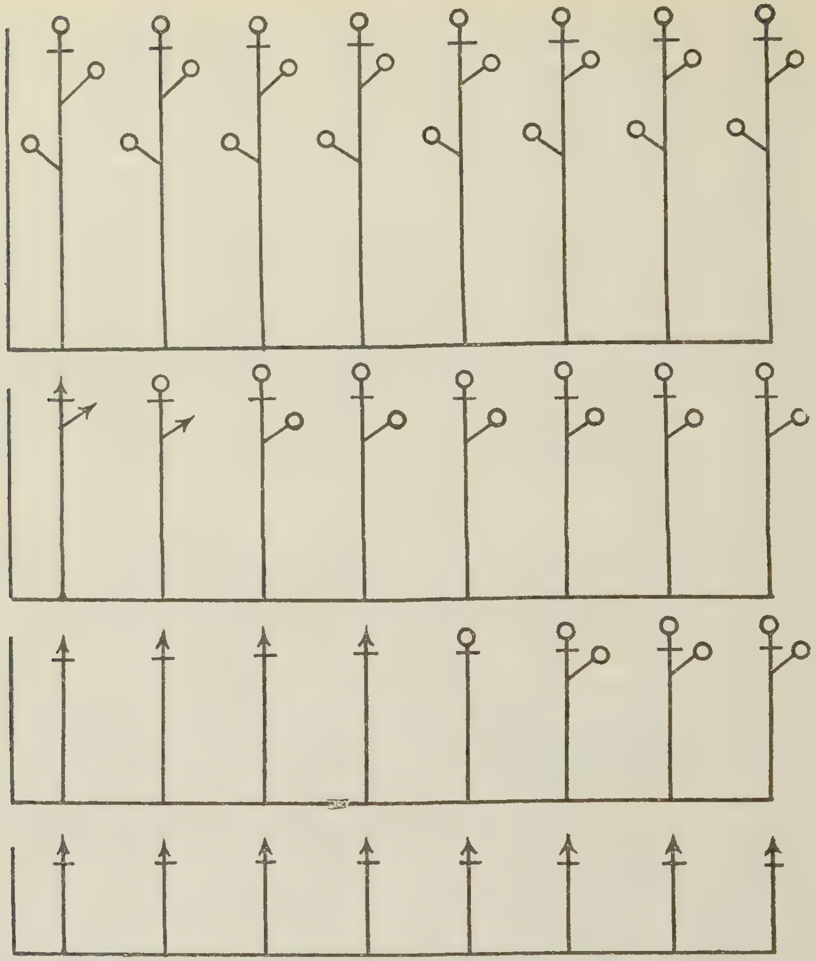

FIG. 2.—Effects of age on initiation of flowers in buds of raspberry shoots subjected to various periods of inductive conditions (10° C and 9 hour daylength) favourable to the initiation of flowers, followed by 6 weeks at 3° C to break dormancy and finally warm light conditions to induce buds to grow.

Key : ↑ — apex resumed vegetative growth.

↗ — lateral bud produced vegetative shoot.

♀ — apex produced terminal inflorescence.

⊸ — lateral bud produced infloresceenc.

DISCUSSION

It is clear from the results of these experiments that length of day and temperature profoundly affect the major phenomena concerned in the development of raspberry shoots, including the beginning and end of the vegetative growth of a shoot, and the onset and breaking of any period of temporary dormancy which interrupts that growth ; the initiation of flowers ; the breaking of dormancy of the flower buds ; and the subsequent development of those buds into flowering branches.

But it is equally clear that shoots do not always repond in the same way to any particular set of environmental conditions. For instance, the terminal meristems of young shoots can pass through a dormant phase without flowers being initiated, whereas the same conditions a season later in the life of the same shoot cause its apex to become floriferous. Similarly, shoots cease to elongate and develop terminal clusters of leaves when subjected to relatively low temperatures and short days, but ultimately start to elongate again if left for long periods of time without changing the environmental conditions.

The concept of ' ripeness to flower ' has long been accepted as meaningful. Perhaps this concept should be extended to all developmental phases, not only to flowering, to become ' ripeness to proceed to the next phase ', whether vegetative or flowering. In many of the phenomena described in this paper it appears that ' ripeness to proceed ' is associated with the effect of environment, in a form of ' dual control '. It could be argued that there is a set of environmental conditions that is particularly favourable to each phase of development. The plant cannot pass into that phase until it is ' ripe to proceed ', however favourable the environment, but once it has reached that stage it will pass rapidly into the new phase provided environmental conditions are suitable. Unsuitable conditions delay that passage, perhaps for prolonged periods of time, but the inhibiting effect of the unsuitable environment appears to decline with the passage of time so that, for instance, a shoot ultimately passes to the next phase—provided it survives for long enough—despite adverse environmental conditions.

Conclusions

More work of this kind is needed, with other species, based first on a definition of the phases of growth in the field and, second, on experimental work in controlled environments. Such work should throw useful and interesting light on the effects of weather on plants, and might ultimately lead to important advances in agronomy.

However, rather little can be done to alter factors of the weather on a field scale, and a more elegant approach to increasing yields would be to alter the plant's responses to weather, so that it grows better, and produces heavier yields, under weather conditions that are suboptimal for the crop and variety concerned. That might be of particular advantage in temperate climates, where late springs tend to delay early growth and prevent plants from taking full advantage of more favourable conditions in the summer months. For instance, it might be useful to be able to increase the number of expanding leaves in the early part of a growing season, or to cause individual leaves to grow more rapidly, so that the leaf area is greater by the time growing conditions improve in early summer.

There is evidence from the present work (Hudson, 1958) that it is possible to alter some responses to weather by suitable chemical treatment, e.g. by the use of gibberellic acid on raspberry plants in the rosette condition (Phase 3), which causes plants to start to grow at once under conditions which would normally prevent growth for long periods of time. It is probable that other plant responses could also be affected by chemical regulators, but there is need for much more precise knowledge about the relations between plants and the weather before this approach could be of any conceivable value in agriculture.

The use of chemical regulators on an agricultural scale could only be successful if (a) the successive phases of development and growth have been fully described, (b) the weather conditions that affect each phase have been worked out, and (c) the effects of the regulators are understood in relation to phase of growth and the weather. Since chemical treatment would be aimed, in effect, at altering the balance of the internal regulatory system of plants, it would require a subtle and well-informed approach but offers interesting possibilities in the field of agronomy.

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4. THE EXPERIMENTAL CONTROL OF SEXUALITY AND INFLORESCENCE STRUCTURE IN ZEA MAYS L.

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(With 3 Plates and 4 Text-figures)

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INTRODUCTION

ALTHOUGH the monoecism of *Zea mays* is normally so perfect as to form one of the most characteristic features of the species, it is nevertheless readily modified by a variety of environmental influences. Photoperiod (Schaffner, 1927, 1930, 1933 & 1935; Choudri and Krishan, 1946) temperature (Richey and Sprague, 1932; Went, 1957) and soil conditions (Sabinin, 1937; Minina, 1938) may all contribute to altering the familiar distribution of staminate flowers in the apical inflorescence (the tassel) and pistillate ones in the laterals (the cobs), whilst mutilation may totally destroy the usual segregation of the sexes so that mixed inflorescences arise (Blaringhem, 1906 a & b ; Petru and Retovsky, 1957). The evidence of abnormal inflorescences of spontaneous origin has been used from time to time in interpreting the homologies of the cob, but in spite of the ease with which structural changes can be provoked there have been few significant attempts to apply experimental methods to analyse the reproductive morphology of the plant in detail, or to seek an understanding of the physiology of its remarkable monoecism. With a number of other polygamous grasses of the Andropogoneae and Maydeae, maize has been used in studies on sex differentiation at Belfast during the last five years. The present paper is a progress report on some of this work on floral morphogenesis in maize ; in it I shall describe experiments illustrating the effects of daylength, night temperature and auxin treatment, and also consider some of the morphological implications of experimentally induced structural changes.

MATERIALS AND METHODS

All of the experiments described in this paper were carried out with the cultivar Golden Bantam. Caryopses were germinated in flats, and seedlings transferred at the emergence of the first leaf to individual 5-in. plastic pots. Except in some of the earlier experiments, they were grown in a mixture of sharp sand and peat, with a ration of a standard nutrient solution supplied at three-day intervals. The pots were watered to run-off on the intervening days. Except where stated, the experiments were carried out in air-conditioned growth chambers with conditions maintained within the limits indicated.

EFFECTS OF DAYLENGTH AND NIGHT TEMPERATURE

Sex Expression

The characteristic effects of photoperiod and temperature may be illustrated by the results of a factorial experiment with two daylengths and two levels of night temperature. This experiment was carried out during November to March, and all plants received 8 hrs of natural winter daylight. Those under short-day treatment were transferred to dark chambers for the remainder of each day, while those receiving long days were given supplementary light at 50–100 f.c. from incandescent sources to provide a total daylength of 21–22 hrs. Air temperatures were regulated above 22° C. during the period under natural daylight, i.e. for 8 hrs of the daily cycle. Plants experiencing warm ‘ nights ’ remained in the same air temperature during the rest of the cycle, while those receiving ‘ cool ’ nights were transferred to cooled chambers at 10° C. for 16 hrs, whether or not additional light was being supplied. Relative humidity was held above 75 per cent, except in the cooled chambers, where it frequently fell to *c.* 50 per cent during the course of the ‘ night ’.

Means and analyses of variance are given in Table I for (a) leaf number on the principal axis, and (b) number of ovaries formed in the male inflorescence (tassel) whether in stalked or sessile, female or hermaphrodite flowers. The number of nodes differentiated on the main axis before the initiation of the tassel is evidently primarily dependent upon daylength. No effect is attributable to night temperature alone, but the significant interaction term suggests that the influence of daylength is greater with cool nights than with warm. The effect of short days in advancing flowering in maize is well known (Schaffner, 1927 ; Roberts and Struckmeyer, 1938), although unlike its relative, *Euchlena mexicana*, maize cannot be restrained from eventual flowering in long days.

TABLE I.—Effects of daylength and night temperature on number of leaves on the main stem and sexuality of the tassel in *Zea mays*. Six replicates per treatment.

Night temperature	Mean No. of leaves on the main stem Daylength		Mean No. of female flowers in the tassel Daylength	
	8 hrs	21–22 hrs	8 hrs	21–22 hrs
22° C.	9·00	12·17	5·67	0·00
10° C.	8·33	13·33	12·50	1·17

Source	Analysis of variance		
	Degrees of freedom	Mean square	
		Leaf number	Female flower number
Night temperature	1	0·38	96·00[1]
Daylength	1	100·04[2]	433·50[2]
Interaction	1	5·05[1]	48·17
Replicates	20	0·88	14·83

[1] $p < 0·05$; [2] $p < 0·01$

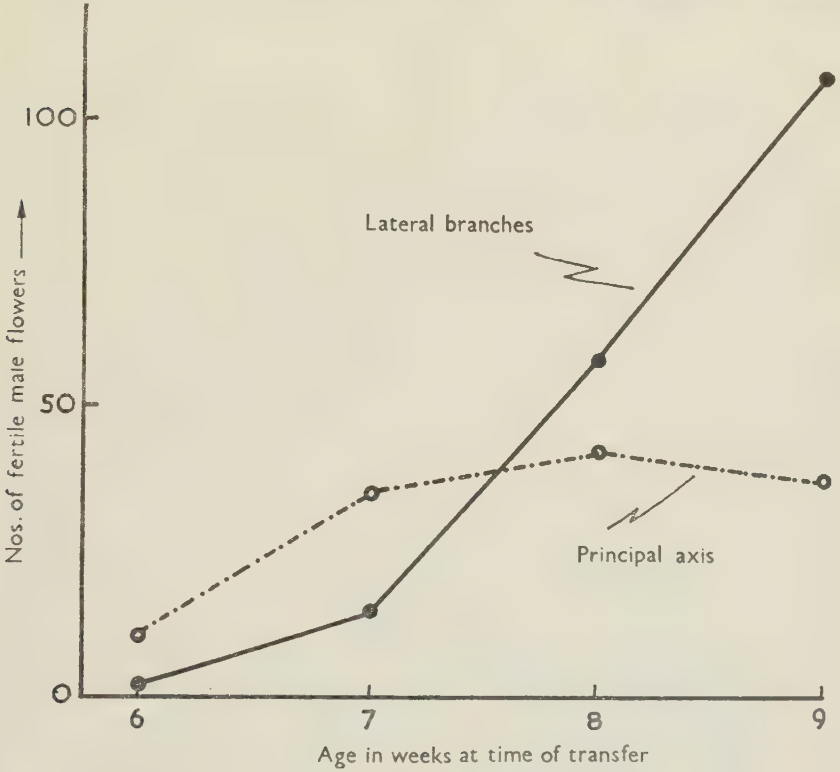
The data of Table I concerning the modification of flower sexuality in the tassel reveal the striking effect of short days in inducing the development of the gynoecial primordia in flowers which would otherwise be wholly staminate. The contributory effect of low night temperatures, noted by Richey and Sprague (1932), is also evident. In long days with warm nights, sex expression, so far as the tassel is concerned, is normal.

Male Fertility

In plants exposed to daylengths and temperatures causing the formation of pistillate flowers in the tassel, there is often also a reduction in the fertility of male flowers. In the extreme case no fertile anthers may be produced at all, so that the plant is functionally wholly female. Although related, these effects—on sex expression and male fertility—can be separated, since pollen production can be influenced environmentally in the flowers of the tassel in comparatively late stages of differentiation at a period when the development of gynoecial rudiments can no longer be induced.

In an experiment to investigate this, plants were transferred at different times during the formation of the tassel from conditions allowing normal pollen formation to those known to produce some degree of sterility. From a matched batch of plants growing in a daylength exceeding 22 hrs (eight hours of natural spring daylight with supplementary light from an incandescent source at *c.* 100 f.c.) with a night temperature of 22° C. and a relative humidity held above 75 per cent, samples were taken at intervals for dissection to determine the state of differentiation of the stem apex. Upon the initiation of recognizable flower primordia on the lateral branches of the tassel, a first group of eight plants was transferred from the long-day, warm-night conditions to short days of 8 hrs natural daylight with a dark-period temperature of 10° C. Thereafter three further batches of eight plants were transferred at weekly intervals to the short-day, cool-night conditions, samples being taken at the time of transfer to observe the state of development of the tassel.

No pistillate flowers appeared in the apical inflorescence in any series, although the conditions of daylength and night temperature after transfer were such as to provoke the development of gynoecia in the tassel if experienced in the period preceding the initiation of the tassel. From this it may be concluded that the sexuality of flowers differentiated as far as the youngest of the lateral branches of the tassel at the time of transfer cannot be influenced by this treatment. On the other hand, the fertility of the male flowers was strongly influenced. Fertility was assessed at the end of the growing season from the total numbers of flowers from which pollen was shed, the principal axis of the male inflorescence and its lateral branches being recorded separately. The observations are summarized in Text-fig. 1.



Text-Fig. 1.—Numbers of fertile male flowers on principal axis and lateral branches of tassels of *Zea mays* following exposure to short days and low night temperatures from the ages indicated.

Evidently in the very young tassel the fertility of flowers both on the principal axis and the branches is depressed by exposure to the short-day, cool-night conditions after previous growth in long days with warm nights. As the age of the tassel advances, it seems that the numbers of susceptible flowers on both principal axis and branches diminish. After the condition of Plate Ia, the flowers of the main axis cannot be influenced, whilst the younger ones of the branches may still be affected ; in later stages those of the branches also cease to be susceptible. A month after the initiation of the tassel in long days with warm nights, the fertility of the male flowers is barely influenced at all by exposure to short days and cool nights. The dependence of susceptibility of the flower primordia upon age is reflected also in the distribution of fertile flower upon the main axis and branches of partly sterile tassels. The flowers of branches develop normally in acropetal succession, whilst those of the main axis develop centrifugally. In consequence the first primordia to become immune to the effects of short-day and cool-night treatment are the central ones of the main axis and the basal ones of its branches (Plate 1b, c).

Effects of Auxin

It is now well established that floral morphogenesis may be modified by auxin treatment in several monoclinous and diclinous dicotyledons (Heslop-Harrison, 1959). The effect is consistently such as to shift the balance of sex expression towards femaleness when auxin levels in the neighbourhood of developing flower primordia are artificially raised, in monoclinous flowers by the promotion of the gynoecium and the suppression of the androecium. There is good reason therefore to expect that the sex distribution in maize can be modified through auxin treatment, and this has now been demonstrated.

The first experiments, carried out in 1956/7, showed an effect of the auxin α-naphthaleneacetic acid (NAA) upon the number of nodes formed before the initiation of the tassel, and upon the position of the first developing female inflorescence. Caryopses were germinated in vermiculite, and the seedlings were transplanted at an age of six or seven days to a mixture of sand and peat where they received a standard ration of a nutrient solution on alternate days. The plants were grown in an orthodox greenhouse, with air temperature maintained over 22° C. throughout but with no control over maximum day temperature. During long-day treatment, they received all available natural daylight and supplementary illumination from a mercury vapour source at an intensity of 300–400 f.c. to give a total duration of 20–22 hrs per day. Plants receiving short days were enclosed in ventilated dark chambers from 5 p.m. to 9 a.m. daily.

The auxin was introduced in aqueous solution containing 50 mgm/l. by the method of Leopold and Thimann (1949). As the fourth leaf was emerging, the apical 2 cm. of the third leaf was removed, and the lamina bent over until the cut surface could be immersed in the auxin solution in a polythene vial alongside the plant. In the course of five days the liquid level in the vial fell to an extent indicating the uptake of 0·4–0·6 ml., allowing for evaporation. The amount of NAA entering each treated plant may be estimated as lying between 20 and 30 μgm.

The results of two experiments using this method are recorded in Table II. The first, carried out during spring and early summer, was of factorial design with five plants per combination of treatments ; the second, conducted during autumn and winter, was a direct study of the effect of auxin under long days, with twenty plants per treatment. Except in the short-day series of the first experiment, the male inflorescence emerged earlier in NAA-treated plants than in the controls by 4 to 7 days, and anthesis, although much more variable in time, was advanced on the average by a similar amount. Time-to-flower is not the most satisfactory measure of developmental rate in monocotyledons of determinate growth, and a better index is provided by plastochron number. The effects of NAA may be judged in these terms from Table II in which the numbers of foliage leaves before the initiation of the tassel and of the nodes at which the first developing female inflorescence appeared are recorded. The analyses of variance for the first experiment shows that short days and auxin treatment were both effective in reducing the number of foliage leaves produced

TABLE II.—Effect of injected auxin (α-napththaleneacetic acid) upon the position of the first developing female inflorescences and the number of leaves on the main stem in *Zea mays.*

Expt. 1. Daylengths of 8 hrs and 20–22 hrs ; five replicates per treatment

	Mean no. of leaves on the main stem Daylength		Mean node with first female inflorescence Daylength	
	8 hrs	20–22 hrs	8 hrs	20–22 hrs
NAA-treated	9·2	10·2	5·6	5·4
Control	9·8	12·8	5·8	8·2

Source	Analysis of variance		
	Degrees of freedom	Mean square	
		Leaf number	Female inflorescence
NAA-treatment	1	12·80[2]	11·25[2]
Daylength	1	20·00[2]	6·05[2]
Interaction	1	37·80[2]	8·45[2]
Replicates	16	0·45	0·25

[2] $p < 0{\cdot}01$

Expt. 12. Daylength 20–22 hrs ; twenty replicates per treatment

	Mean no. of leaves on the main stem	Mean node with first female inflorescence
NAA-treated	$10{\cdot}3 \pm 0{\cdot}10$	$5{\cdot}4 \pm 0{\cdot}16$
Control	$11{\cdot}7 \pm 0{\cdot}13$	$6{\cdot}2 \pm 0{\cdot}15$
	$t = 8{\cdot}045,\ p < 0{\cdot}01$	$t = 3{\cdot}337,\ p < 0{\cdot}02$

and in lowering the node at which the first ear developed. The significance of the interaction term in each case indicates that the effects are not simply additive. In respect to the positions of both male and female inflorescences, the effect of auxin treatment is most apparent under long days—or, looked at from the other viewpoint, is masked under short days. In the second experiment, NAA-treatment also significantly advanced the nodes at which inflorescences of each sex were formed under long days, although the difference was less marked than in the corresponding groups of the earlier experiment. It seems probable that this is attributable to the lower intensity of daylight during the period of the second experiment, which was conducted during autumn and winter.

As already mentioned, previous work on the flowering behaviour of maize has shown development to be accelerated by short days, an effect clearly seen in the present experiments. Gausman and Dungan (1954) have reported a retardation of anthesis in maize following massive NAA-dosage before the differentiation of the male inflorescence ; they do not, however, provide data concerning plastochron number or photoperiodic conditions. Leopold and

Guernsey (1953) have observed an acceleration of development towards flowering in maize of a similar order of magnitude to that recorded here after the caryopses had been soaked in solutions of NAA of strengths 0·001 to 1 mgm/l., but only if the auxin treatment was followed by a brief exposure to low temperature (3° C.). The photoperiod under which this result was obtained is not specified.

These first experiments gave no indication of an effect of auxin upon the sexuality of the flowers, and further experiments were carried out during 1958/59 under more closely controlled conditions. Daylength conditions were chosen for the period preceding and during treatment which were themselves marginal for the production of sexuality modified tassels, with the intention of emphasizing any shift in the balance of sex expression. The plants were grown in growth chambers with a constant air temperature of 22° C. and a relative humidity of 75 per cent under a daylength of 10 hrs, light being supplied at an intensity of 900–1100 f.c. from batteries of warm-white fluorescent tubes. Four groups of eight plants were assembled and closely matched for uniformity when the third leaf had reached a length of 5–8 cm., at which stage in the prevailing daylength the growing point in the cultivar Golden Bantam is still vegetative. The auxin, NAA in aqueous solution at 100 mgm/l., was administered to the plants of two groups by injection with a micro-pipette into the cavity formed by the younger leaves immediately above the growing points, each plant receiving *c.* 0·15 ml. per dose. Four such treatments were given over a period of four weeks, spanning, as previous experience had indicated, the period of differentiation of the tassel. Two days after the final treatment, one treated and one untreated group were transferred to an 8-hr day, and one treated and one untreated group to a 20-hr day, air temperature and relative humidity remaining unchanged.

Means and analyses of variance for two variables, numbers of female flowers formed in the tassels and numbers of tassel branches, are given for the four combinations of treatments in Table III. The appearance of some sexually modified tassels in plants of the series not receiving auxin treatment reveals that, as had been intended in the design of the experiment, the conditions of daylength and light intensity experienced prior to and during the period of tassel differentiation were marginal for the induction of gynoecium development in some of its flowers. However, for the combined groups the effect of NAA in causing the formation of female flowers is highly significant. The development of the treated plants was always somewhat retarded, and it could be argued that the effect of the auxin was merely to delay the critical period of differentiation so that it was reached during short days in the group transferred to these conditions. The insignificance of the daylength and interaction terms eliminates this possibility, and indicates that the observed effect is wholly attributable to the auxin treatment.

The second principal effect of auxin treatment is the suppression of branching in the tassels, many of which were composed of a single axis only (Plate 1d). Again the effect is wholly attributable to the auxin and not at all to daylength in the post-treatment period. The significance of this modification of the structure of the male inflorescence—itself an indication of a shift towards the organization characteristic of the female—is discussed further below.

Superimposed upon the principal effects in this experiment was that upon male fertility to be expected in those plants transferred to short days after the initiation of the tassel. Observations upon male fertility were not made in a form permitting full analysis, and the result can therefore be given only in general terms. Of the auxin treated series, those subsequently receiving long days were male fertile, although due to the reduction in the numbers of tassel branches the total numbers of flowers and thus pollen output were much re-

Table III.—Effect of auxin (α-naphthaleneacetic acid) on the formation of lateral branches and female flowers in the tassel of *Zea mays*. A, daylength of 8 hrs after treatment; B, daylength of 20 hrs after treatment. Six plants per treatment.

	Mean no. of branches		Mean no. of female flowers	
	Daylength		Daylength	
	8 hrs	20 hrs	8 hrs	20 hrs
NAA-treated	1·17	0·33	5·67	3·17
Control	8·17	7·17	0·83	0·17

Source	Analysis of variance		
	Degrees of freedom	Mean square	
		Branches	Female flowers
NAA-treatment	1	287·04[2]	92·04[2]
Daylength	1	5·04	15·04
Interaction	1	0·04	5·04
Replicates	20	3·39	6·59

[2] $p < 0{\cdot}01$

duced (Plates 1e, 2a). Most of the treated plants transferred to short days were wholly male sterile (Plate 2b), and those showing some fertility commonly produced only a few flowers in the central region of the inflorescence. Of the untreated plants, those in long days after the initial period of 10-hr days showed normal fertility (Plate 1f), whilst those in short days showed some slight sterility only on the lateral branches. Although it may be suspected that NAA may exert a direct effect upon male fertility, the design of this experiment was not such as to expose it unequivocally, since the difference in male fertility between the treated and untreated plants under short days may be attributable not to a specific effect of the auxin on microsporogenesis but to its delaying effect on development, which ensured that plants of the treated series entered the short-day regime with tassel primordia in a much earlier state of differentiation than in the untreated.

Structure and Homologies of the Male and Female Inflorescences

Accounts of the development and structure of the normal flowers and inflorescences have been given by numerous authors, in varying degrees of detail (e.g., Weatherwax, 1916, 1917, 1931, 1955; Collins, 1919; Miller, 1919; Arber, 1934; Randolph, 1936; Fujita, 1939; Anderson, 1944; Mangelsdorf, 1945; Cutler and Cutler, 1948; Reeves, 1946, 1950; Hayward, 1954; Nickerson, 1954). The studies of Bonnett (1940, reprinted with minor amendments, 1948) are among the most comprehensive in respect to ontogenetic detail. Genetically governed aberrations of floral morphogenesis and sex expression have been listed by Emerson, Beadle and Fraser (1935); among the best known mutant types are the tunicate series (discussed in detail by Mangelsdorf and Reeves, 1959), and silkless (*sk*) and tassel seed (ts_2), used by

Jones (1934, 1939) in the synthesis of a so-called dioecious family. Structural features of inflorescences showing sexual abnormality from genetical causes or exposure to abnormal environments have been described by Blaringhem (1906, 1924) ; Emerson (1920) ; Penzig (1921) ; Weatherwax (1925, 1955) ; Schaffner (1927, 1930, 1933, 1935) ; Arber (1934) ; Bonnett (1940) ; Stephens (1948) ; Galinat and Naylor (1951) ; Petru and Retovsky (1957) ; Mangelsdorf (1958) ; Mangelsdorf and Reeves (1959) and many others.

The Normal Male Inflorescence

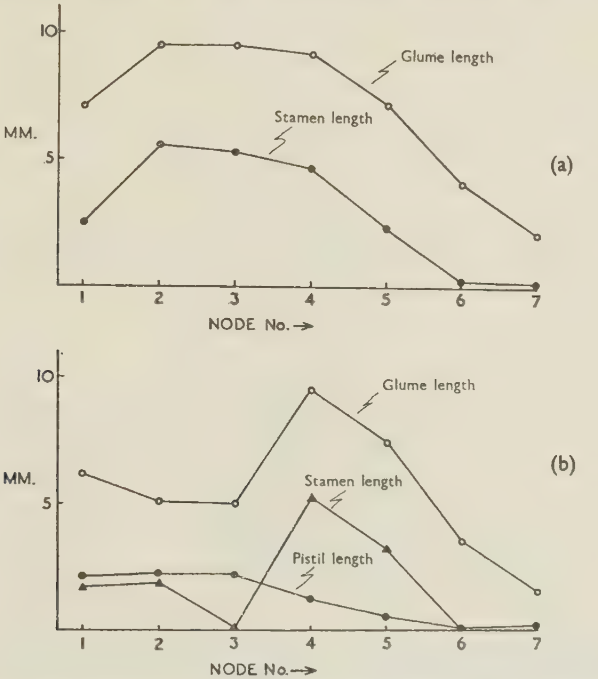
In basic architecture, the male inflorescence of maize resembles that characteristic of the polygamous inflorescences of the Andropogoneae, a tribe from which the Maydeae is distinguished primarily by the condition of monoecism. Each axis may be looked upon as composed of homologous segments or phytomers, bearing usually a group of spikelets, the *alicole* in the sense of Collins (1919). Of the normally paired spikelets of the alicole, one is sessile, and the other pedicellate. Each spikelet is potentially two-flowered, and during ontogeny the upper flower of the rachilla develops first. Occasionally the lower flower fails to mature, leaving the spikelet functionally one-flowered. In the typical monoecious plant the gynoecium remains rudimentary in the flowers of the tassel.

Zonation in Modified Inflorescences

It seems that in some genetical mutants flowers of different sex types may be distributed in a mosaic fashion in the tassel, but wherever sexually modified tassels arise through environmentally governed developmental aberrations it is usual for male and female flowers to be distributed in some fairly regular pattern of zonation.

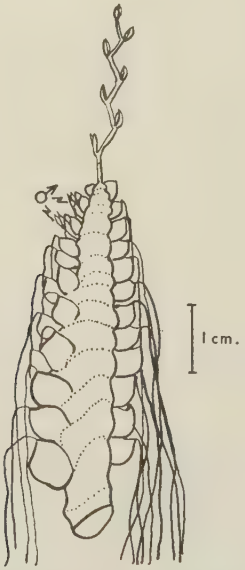
The commonest type of zonation, and that exclusively found in plants grown under the controlled conditions of the experiments described above, is one in which the female flowers are restricted to the lower parts of the principal axis or its branches, the apical flowers being morphologically male, although not necessarily functional. A plant from the series experiencing short days and warm nights in the first experiment described above may be used to illustrate the regularity of the zonation. In this individual, the unbranched apical inflorescence was of nine nodes, and contained structurally perfect male, female and hermaphrodite flowers (Plate 2c). Some salient dimensions are summarized in Text-fig. 2. In the three basal sessile spikelets, both flowers were structurally female, each with extended styles. The length of the glumes of these spikelets was equivalent to that of the glumes of the spikelets of the normal cob, and they possessed the same membranous texture ; this is generally true whenever wholly female flowers are formed in the tassel. The sessile spikelets at the succeeding two nodes contained each one hermaphrodite upper and one aborted lower flower. In the hermaphrodite flowers, the moderately well-developed gynoecium was accompanied by an androecium and with well formed pollen, and the glumes were of a length and shape similar to that of male flowers, with the same venation and texture (cf. Plate 2d). The pedicellate spikelet at the lowest node of the inflorescence was structurally male, but the anthers of both flowers had aborted. At the succeeding three nodes, both flowers of the pedicellate spikelets were fertile males, without discernible gynoecial rudiments. Those at higher nodes were again structurally male, but imperfectly developed.

The structure of this inflorescence shows that notwithstanding the generalization of Bonnett (1940) that gynoecia where present in the tassel only appear in the upper flowers of sessile spikelets, both upper and lower may become functionally female. The transition to femaleness may be even more complete in plants subjected simultaneously to short days and low night temperatures, and inflorescences similar in organization to the cob may be formed at the stem apex under these conditions. In one such plant, the compacted basal part of the inflorescence bore six alicoles, each consisting of one sessile and one very shortly stalked spikelet. All of the sessile spikelets in this part of the inflorescence were female, and also the pedicellate spikelets of the first three alicoles. Those of the upper three were sterile, but with the glume shape characteristic of male spikelets. The uppermost part of this inflorescence was extended, with a total of ten alicoles. Of these, the basal three bore sessile spikelets with single hermaphrodite flowers, and the basal four pedicellate spikelets with paired fertile male flowers. The spikelets of all succeeding alicoles contained structural male but sterile flowers.



Text-Fig. 2.—Over-all lengths of glumes, pistils and stamens of (a) pedicellate, and (b) sessile spikelets at the first seven nodes of a terminal inflorescence of a plant of *Zea mays* experiencing short days with warm nights (cf. Plate 2*c*).

There is a striking agreement between the organization of the basal part of the modified tassel just described and the type of four-rowed cob occasionally formed by this cultivar. In each, paired spikelets, one sessile, the other very shortly stalked, form vertical ranks on two faces of a condensed and somewhat compressed axis. Modified female inflorescences appeared in several plants in the present experiments, some giving still further indications of homology. In plants subjected throughout life to long days with high night temperatures, it was common for lateral female inflorescences to be differentiated at a late node, but not to develop beyond a length of a few millimetres. In one plant, paired, structurally male, inflorescences were differentiated at the seventh node of the main stem, with alicoles similar to those of the normal tassel, but sterile (Plate 3a). In some instances, the apical part of the cob, normally condensed and with rudimentary flowers (Bonnett, 1940) extended to give a slender, often flexous prolongation of the axis, upon which paired sterile spikelets were inserted distichously as in a branch of the tassel. An example is illustrated in Text-fig. 3; here the resemblance to modified tassels such as those described above was increased by the presence of morphologically male flowers in the pedicellate spikelets of two upper alicoles of the condensed portion of the cob. It is noteworthy that in the very young female inflorescence even under normal conditions the flower primordia of the upper and lower portions may differ to some extent at the time when the styles are beginning to extend (Plate 3b). The upper few alicoles show more extended glumes, less well developed gynoecia, and better developed stamens. Normally this male-inclined apical segment undergoes little or no growth.



Text-Fig. 3.—A modified lateral inflorescence, showing the development of the terminal male segment, normally aborted. Male flowers are present in the pedicellate spikelets of two upper alicoles.

Zonation patterns of other kinds have been recorded by various authors, notably Schaffner (1933) and Reeves (1950). Thus there may be more than one change of functional sexuality along the length of the principal axis of the tassel, to give a sequence male→female→male, or female→male→female, with or without intervening zones of sterile flowers. There seems little reason to doubt that Schaffner was correct in attributing this kind of alternation to the fact that development in the principal axis is centrifugal, so that at any time during early growth two bands of flower primordia along the axis may be in the same stage of differentiation. The point is considered further below.

Male→female→male transitions in the main axis of the tassel such as that illustrated by Reeves (1950) are of special significance in interpreting the morphology of the cob. These have not so far arisen in controlled experiment, but one tassel showing the male→female type of transition is illustrated in Plate 3c. This was obtained from a plot of maize in the planting grounds of the Agricultural Experimental Station at Lethbridge, Alberta, in which several individuals showed sexual anomalies, mostly in the form of basipetal zonations of the kinds already described. The female-flowered section of the tassel illustrated in Plate 3c is in all respects identical in organization with a normal cob, showing the same compact arrangement of alicoles. Similarly the basal section corresponds structurally with the main axis of a normal male inflorescence. In both male and female sections, the arrangement was polystichous, with the alicoles in four ranks. There can be no doubt this inflorescence has arisen from a tassel primordium of a perfectly normal character, and that the unusual distribution of sexes has arisen through the development in different zones of androecium or gynoecium in initially monoclinous primordia. From this it may be concluded that there is no feature of the basic structural organization of the cob which is not present also in the central axis of the tassel. The differences which are so striking in the mature inflorescence evidently arise through the establishment of different growth patterns in the axis *after* the commitment of the flower primordia which it bears to one or other developmental pathway ; in particular, the condensation and thickening of the axis and the differentiation within it of supplementary vascular bundles (Reeves, 1950) must be attributed to physiological changes initiated by the development of gynoecia rather than androecia. Maize is in no way unique in this respect ; in many species with diclinous flowers, the inflorescences or portions of inflorescences with female flowers show greater condensation and more massive vasculation than those with males, these secondary sexual characteristics arising after the commitment of the flower primordia.

Branching

Characteristically, the male inflorescences of maize are branched whilst the females are unbranched, facts which have engaged the attention of most of those who have speculated upon the phylogeny of the species and the homologies of the two types of inflorescence (e.g. Weatherwax, 1935 ; Anderson, 1944 ; Mangelsdorf, 1958 ; Cutler and Cutler, 1948). The earlier view that the cob is a product of fasciation or the developmental fusion of a central spike with lateral branches has little to commend it, and the currently more popular view accepts the homology of the central axis of the tassel and the cob, and assumes that the solitary condition of the latter is due to a total suppression of basal branches.

In this connection, the partial or total suppression of branching in the tassel following the administration of NAA in the experiment described above is evidently of significance. It should be emphasized that this is a morphogenetic effect not attributable merely to a failure of the primordia of lateral branches to extend ; there are no vestigial branches at the bases of the uniaxial tassels of auxin-treated plants, as may be seen in Plates 1e and 2a, b. Whether or not there are associated changes in sexuality, the first structure to emerge from the axis of the inflorescence above the last leaf sheath is an alicole. It is apparent, then, that a high level of auxin in the neighbourhood of the stem apex before and during the period of tassel differentiation can produce an inflorescence structure simulating that of the cob, as well as leading to the later development of pistillate instead of staminate flowers.

FLOWER ONTOGENY

The Flower Primordium

The ontogeny of the spikelets and normal flowers of the two sexes in maize has been described in detail by Bonnett (1940). As this author stresses, the initiation of the pairs of spikelets in the alicole follows much the same course in both apical male and lateral female inflorescences ; the differences which at maturity almost wholly conceal the homology of tassel and cob arise through later divergence in the growth rates of pedicels, glumes, pales and axes. The young flower primordia on apical and lateral inflorescences are in fact indistinguishable. In each, the anthers are the first floral parts to be initiated, as eminences on the flanks of the floral meristem ; the differentiation of the gynoecium then begins, the first indication being the initiation of the style as an incomplete lip round the meristem. From this monoclinous condition of the primordium the flowers of the two sexes now rapidly diverge. Under the photoperiodic and temperature regimes experience in the normal spring and early summer period of growth, the gynoecium in the male flower rarely develops beyond a length of 0·5 mm., and the anthers in the female flower rarely grow beyond 0·25 mm., except occasionally towards the apex of the cob, where anthers may develop to the stage of differentiating an archesporium. In general, then, although the flower primordium is of a hermaphrodite pattern, dicliny is established very early , and the mature flowers of each sex show fewer vestiges of the other than, say, those of diclinous dicotyledons like *Melandrium.*

PLATES 1–3

PLATE 1

a. Condition of the tassel at an age of seven weeks in a plant grown in long days with a night temperature of 22° C. (× *c.* 9·5)

b. A developing tassel showing the centrifugal sequence of growth of flower primordia on the central axis. (× *c.* 8·0)

c. Partly sterile tassel of a plant exposed to short days and low night temperatures from an age of seven weeks. The fertile flowers are restricted to the central zone of the main axis, corresponding in position to the most advanced flower primordia seen in Plate 1*b*. (× *c.* 0·5)

d. Tassel of an auxin treated plant, showing the reduction to a single axis. (× *c.* 0·6)

e. Basal part of the tassel illustrated in Plate 1*d*. The sessile flowers of the basal alicoles are female, and the styles are developing. In this plant, exposed to long days after treatment, the male flowers are fertile. (× *c* 4·25)

f. Fertile tassel of a plant grown in long days showing copious basal branching : *cf.* Plate 1*d*, *e*, and Plate 2*a*, *b*. (× *c.* 2·5)

PLATE 2

a. Tassel from auxin-treated plant exposed to long days after treatment. Moderately well developed female flowers basally, and fertile males above. (× *c.* 2·5)

b. Tassel from an auxin-treated plant exposed to short days after treatment. Well developed basal flowers, with sterile males above (× *c.* 2·75)

c. Apical inflorescence from a plant experiencing short days and warm nights, with female, male and hermaphrodite flowers. The sex distribution is described in the text, and dimensions of various organs are summarized in Text-fig. 2*a*, *b*. (× *c.* 2·5)

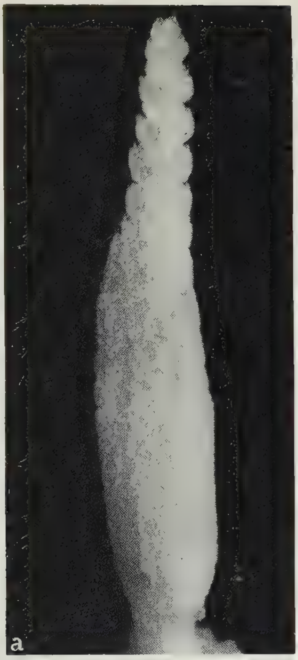
d. An alicole of a terminal inflorescence showing a sessile hermaphrodite spikelet and a pedicellate male one. The glumes of the sessile spikelet are more elongated than in a normal female. (× *c.* 4·5)

PLATE 3

a. Morphologically male but sterile inflorescence formed at the seventh node of the main stem in a plant subjected to long days with high night temperatures. (× *c.* 2·5)

b. Young lateral female inflorescence at the time when the styles are beginning to extend. Upper flower primordia show greater development of glumes and anthers, and less development of the pistils, i.e., they are more male in character. (× *c.* 8·0)

c. Part of a tassel from a plant of *Zea mays* from Lethbridge, Alberta, showing a transition from a zone of fertile male flowers to one of normal females, arranged as in a female inflorescence. (× *c.* 1·6)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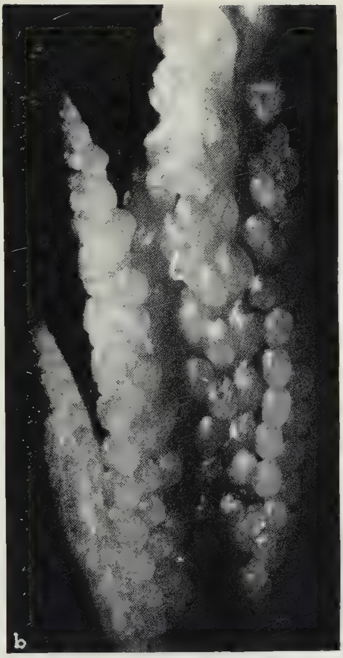
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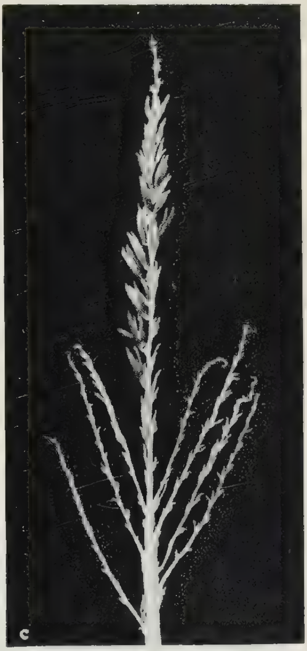
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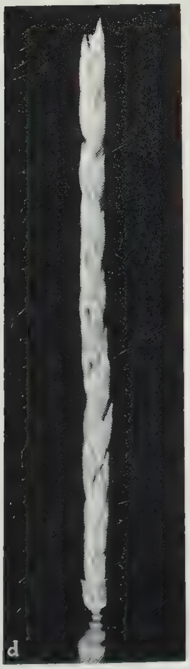
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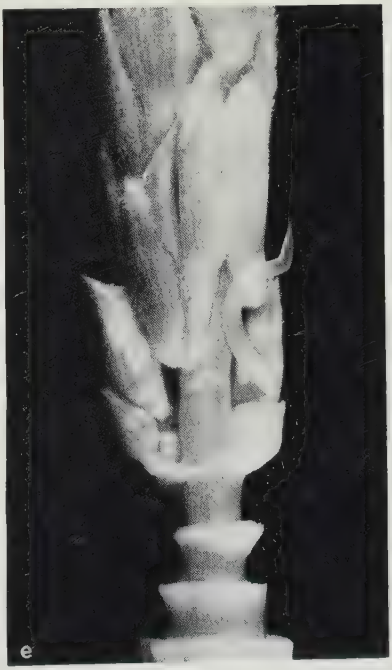
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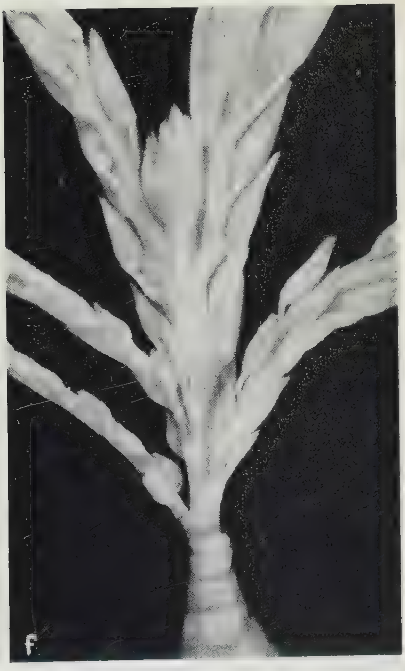
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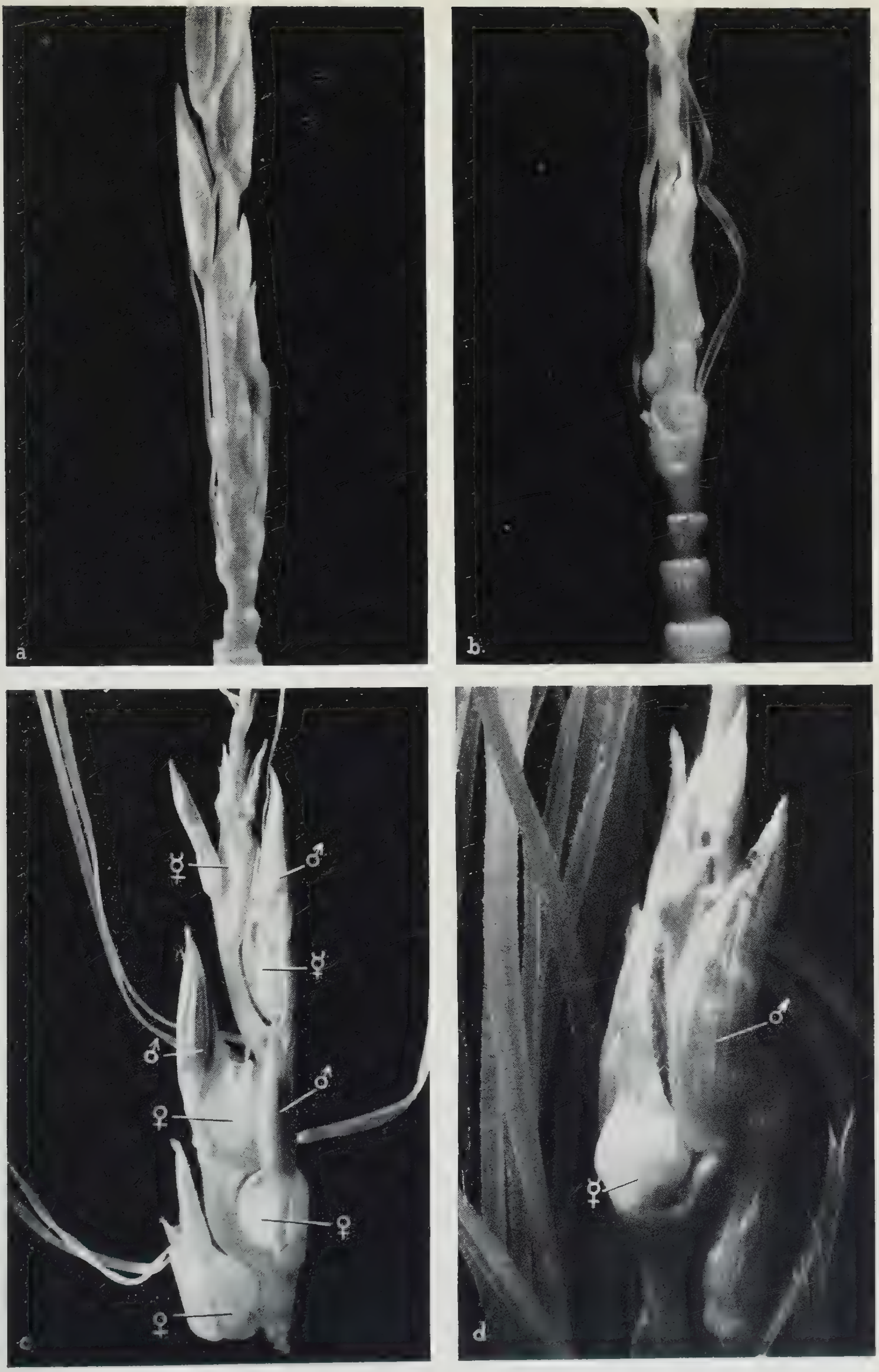
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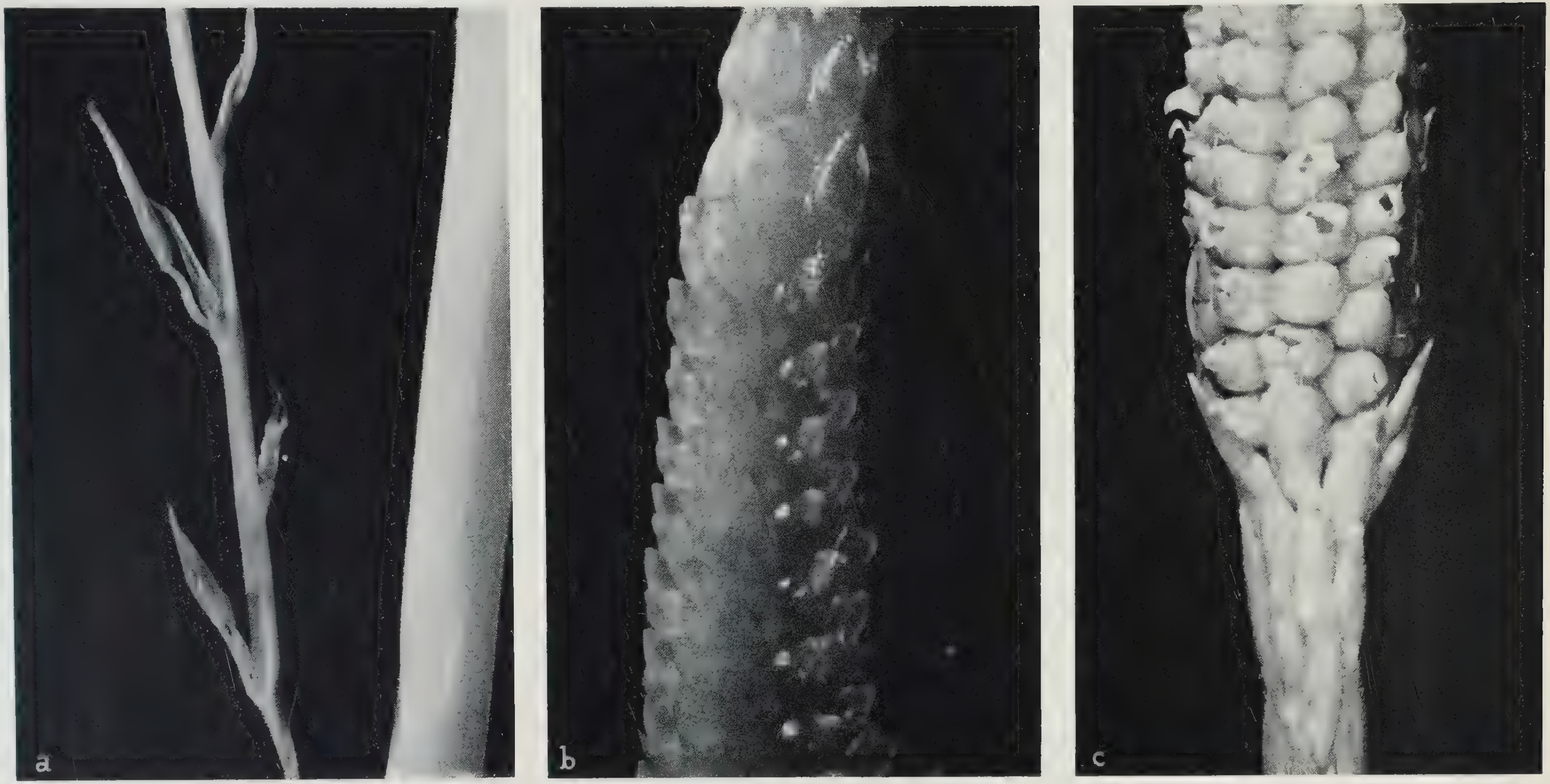
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The Control of Sex Function

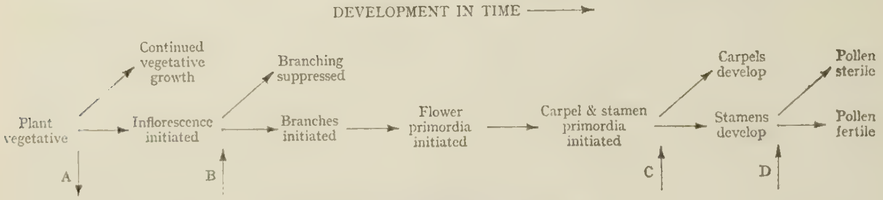
In the 1959 symposium of the Experimental Morphology Group of the Linnean Society, I suggested that it was profitable to look upon the processes of flower morphogenesis as passing through three phases : the inception of the primordia of the floral members, the commitment of each class to their specific paths of development, and finally their outgrowth and differentiation. In the case of the monoecious *Zea mays*, it may be said that the first two of these processes are as in any hermaphrodite grass, and no experimental treatment has as yet caused their modification. Dicliny arises as a change in the balance of growth of the primordia of gynoecium and androecium. In the intact plant in its normal environment conditions are such in the lateral inflorescences as to cause the activation of the gynoecium and the suppression of the androecium, and in the apical one, to promote the development of the androecium and to check that of the gynoecium. It is this balance of growth between the two classes of organs, and nothing more profound, which is affected by such treatments as those described above.

However, these experiments and others of a similar kind not recorded here carry an important implication : that the developmental path in any one flower is determined decisively in the very early stage of differentiation. Thus tassels as young as that illustrated in Plate 1a fail to form female flowers when exposed to suitable inductive conditions. Seemingly at this stage irreversible changes have already taken place which prevent the future growth of the gynoecium even in the flowers of the lateral branches. So far, it has not proved possible to design an experiment of sufficient precision to establish the condition of the primordium at the time of determination, and it could even be that it takes place before the actual emergence of the gynoecial and androecial rudiments from the floral meristem. However, the evidence of tassels showing alternating zones of flowers of each sex suggests that each flower primordium does pass through a phase of competence after its inception, and that during this period determination takes place. The decisive events are clearly local ones, not engaging all the tissues of the young inflorescence.

Although the prospective fate of a flower primordium may be determined early in its life, whether or not the normal developmental path is pursued to its end may depend upon conditions during later growth and differentiation (Heslop-Harrison, 1959). This is well illustrated in maize by the effects of photoperiod and temperature during the later stages of tassel growth on the fertility of male flowers. Short days and low night temperatures are no longer capable of activating the gynoecial primordia in the flowers, but the changes which these conditions produce in the tissues of the primordium can prevent the normal differentiation of stamens and cause a failure of pollen production. But once again it seems that there is only a limited period in the early growth of the flower during which this effect can be produced ; subsequently the stamens cease to respond to the influence of unfavourable environment and continue their normal differentiation and pollen production.

THE FLOWERING PROCESS IN TERMS OF DEVELOPMENTAL PATHWAYS

Evidence such as that reviewed above suggests that it may be profitable to view the whole process of flowering in terms of the selection of alternative developmental pathways. There is no doubt some over-simplification in assuming that a set of strictly successional determinations is involved, but at least the approach is useful in providing an initial perspective. What is known about the behaviour of maize, then, is summarized in these terms in Text-fig. 4. The axial sequence in this diagram represents the normal developmental path leading to the production of a fertile male inflorescence in a plant germinating in spring and flowering in late spring and early summer. The alternative developmental pathways open at different times are indicated, together with the treatments known from experiment to affect their choice. Reasons for supposing that the various environmental treatments might be effective through their influence upon native auxin metabolism have been reviewed elsewhere (Heslop-Harrison, 1957*a*, 1957*b*, 1959) : obviously it must now be a task to demonstrate this experimentally. Perhaps it does not require emphasis that such a demonstration would, however, contribute merely to clearing the air ; the more basic problems would remain of how alternative gene systems are activated or deactivated through hormonal control, and of how they govern morphogenesis.



Alternative developmental paths in the flowering of *Zea mays*. The axial sequence represents the developmental route leading to the formation of a fertile male inflorescence in a normal annual cycle of growth. At A, B, C & D the developmental pathway may be switched in the direction indicated by short days, low temperature treatments or auxin administration.

TEXT-FIG 4

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the help of my wife, Dr Y. Heslop-Harrison, in all phases of this work. My thanks are due also to Mr R. B. Knox, B.Sc., who did some of the scoring in the experiment on male fertility, and to Mr R. Johnson, for his devoted care of the plants.

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5. FACTORS AFFECTING FLOWER INITIATION IN CERTAIN CONIFERS

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The factors which affect flowering in coniferous trees have received little attention until recent years, and there is not yet a great deal more known about the morphological changes which occur at the apex when reproductive organs are formed. It must therefore be made clear at the outset that the investigations described here are in an early, exploratory phase.

It is in some ways rather surprising that so little is known about the flowering of conifers, and some explanation may not therefore be out of place. In a number of ways experimentation with coniferous trees is difficult. For instance, the material is genetically very variable, there having been practically no systematic breeding of conifers in this country until the last decade. A second more important point is the existence of a juvenile or non-flowering period in the life of the tree, in some conifers as long as 25–30 years. Investigation of flowering is therefore complicated, since a factor which affects flowering in a mature tree need not necessarily affect the change from the juvenile to the mature phase, and *vice versa*. Furthermore, by the time that flowering commences most conifers are too large to grow under controlled environments, and it may even be necessary to climb the tree to reach the flowers. Moreover, the shoot system has by this time become complex, imparting a certain lack of precision to experiments.

Previous studies on the initiation of flowering in other groups of plants, such as fruit trees and ornamental shrubs, suggested that such factors as temperature, day-length and manurial status might be involved. Effects on flowering have, in fact, been found with several different treatments, but attention will be concentrated here on the effect of gravity. That the force of gravity might influence flowering in woody species was suggested in the first place by horticultural practice, rather than by previous experimentation. For example, techniques of training fruit trees in France and Germany involving the pulling over or 'arching' of vertical shoots are claimed to reduce vegetative growth and increase flowering. Wareing & Nasr (1958) have shown experimentally that to grow varieties of apple horizontally leads to a great increase in flowering, and they were able to demonstrate that the important factor was the orientation of the shoot relative to gravity.

A further interest in gravity was stimulated by a study of the morphological position of flower buds in Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gordon). These are initiated in the early summer, and then emerge in February or March of the following year. It was noticed that the male flower buds occurred mainly on twigs orientated horizontally or below ; and that their arrangement on these twigs was rather striking. The majority of flower buds were to be found on the *lower* sides of more or less horizontal twigs, and on *all* sides of the trailing twigs which are common in this genus. In general, therefore, the flower buds themselves may be expected to point downwards on the horizontal twigs, and horizontally on the trailing twigs.

An assessment of more than 300 male flower buds showed that 98 per cent of them pointed either horizontally or below. None was found pointing directly upwards. These measurements abundantly confirmed the observations on the morphological position of the male flower buds in larch, and this distribution in fact appears to be a regular feature of this genus. It was not yet clear, however, whether these results indicated an effect of gravity, or whether the flower buds occupied the lower side of horizontal shoots because of some inner, ‘ fixed ’ feature of the abaxial side of the shoot.

In a preliminary experiment it was found that male flower buds could be induced on the upper or adaxial side of a shoot simply by inverting the whole top of the tree. A more precise experiment was carried out in a subsequent year, using material in which flower buds were already detectable macroscopically, though sporophyll primordia had not yet been initiated. Horizontal twigs, bearing presumptive flower buds on their lower sides, were bent and fixed in such a position that the distal part was completely inverted, while still remaining in a horizontal plane.

In each of six such twigs, flower buds subsequently developed on the original upper side, now situated below ; while on the original lower side some at least of the presumptive flower buds developed as vegetative buds. In the corresponding control pairs, flower bud distribution was normal. It is evident that, during the early stages of bud initiation, it is possible to convert a developing vegetative bud into a flower bud, and *vice versa*. More important, this experiment indicates that a direct gravitational stimulus is involved in the determination of floral structures in larch.

Certain observations suggested that gravity might also be one of the factors concerned in the attainment of the mature condition in larch. Young trees of this genus frequently have branches which curve strongly upwards, on which flowering has generally not started. As the branches become older, they frequently come to lie more horizontally, and the first appreciable flowering occurs. Later, branches may even come to point downwards, although at the top of the tree the new branches are often upswept for many years.

Clearly, any such ‘ sagging ’ of the branches will result in more and more twigs and buds pointing horizontally and below : that is, in a potentially flowering position, and a correlation between changing branch orientation and the onset of flowering is therefore suggested. Accordingly, a series of experiments was started in which branches were experimentally pulled down and tied either horizontally or in a downwardly pointing position. Young trees were chosen which had borne few or no flowers to date, and the treatments were applied in March and April to branches two to five years old.

A marked effect was produced by both the training treatments in eight out of twelve trees, and a smaller effect in two more. An average of 90 flowers in the tied down branches and 50 in the horizontal compare with few or none in the equivalent control branches. There was considerable variation in the material, but significant differences were shown from the controls in both cases. Moreover, since in several cases the whole of the rest of the treated trees bore no flowers, pulling the branches down has undoubtedly advanced the onset of appreciable flowering by one to two years at least. It therefore appears probable that in nature the gradual ‘ sagging ’ of branches will favour the onset of flowering. Other factors are doubtless involved as well, and may modify the response to gravity. For instance, the weather of the early summer of 1957, in which year this experiment was carried out, was warm and sunny, which is apparently favourable for flower initiation. 1958, on the other hand, was a cool, wet summer, and there were only a few flowers induced in a second experiment. In 1959, however, there was again a large effect of tying down.

It is clear that these effects of gravity on flowering cannot aptly be described under the heading of geotropism. Moreover, although there were marked reductions in shoot growth in all treatments involving horizontal and downwardly directed branches, this was not necessarily associated with any growth curvatures. The term ‘ gravimorphism ’ has been proposed (Wareing & Nasr, 1958) to cover all such morphological rather than tropic responses. One may then speak of ‘gravimorphic treatments’ with the same implication as, for example, ‘ photoperiodic treatments ’.

As regards a possible mechanism for these gravimorphic effects in larch, it is too early to do more than make certain observations. It is widely held that both geotropic curvature and apical dominance are brought about by differential distribution of growth hormones, and in some herbaceous plants flowering is thought to be similarly controlled. In this connection, the work of Nečesaný (1958) is of considerable interest. He has reported finding a preponderance of growth-promoting substances in extracts of cambium and young xylem elements of the lower side of horizontal pine shoots. The upper side of these horizontal shoots contained more inhibitors.

A similar technique is to be tested with larch, and an attempt made to relate the findings with the flowering effects. Meanwhile, some circumstantial evidence was provided by the experiment in which horizontal shoots were inverted. When twigs were sectioned it was found that there had been an effect on the position of compression wood, an abnormal type of xylem which is very commonly found on the lower sides of coniferous branches. Compression wood had evidently commenced before the twigs in question were inverted, but it ceased abruptly upon treatment and recommenced on the new lower side. There is thus a possibility that the floral stimulus and the compression wood stimulus were similar, or even the same, since both ‘ migrated ’ round the twig within a few days or a week when the twig was inverted. Nečesaný’s claim that he could stimulate compression wood formation by applying synthetic indoleacetic acid lends some further weight to this hypothesis.

To sum up, therefore, gravity has been shown in a number of experiments to influence the flowering and shoot growth of Japanese larch, and it may be that natural changes in branch orientation have similar effects. It appears likely that effects of gravity will also be found with other genera of conifers. Amongst Angiosperms marked effects of gravimorphic treatment on flowering have been found with apple, and smaller effects with cherry (Wareing & Nasr, 1958). On the other hand, birch and plum trees showed no such effects on flowering, though shoot growth was reduced as in larch.

In conclusion, some mention may be made of studies on the effects of other environmental factors. Temperature and day-length have been clearly shown to affect flower initiation of *Pinus contorta*. Young potted trees of this species formed substantially more female cones under short-days than under natural day-lengths, provided that the plants were grown out-of-doors. Under greenhouse conditions, no female cones at all were initiated under short-days over a period of three years.

Another technique which has often been used with success is the old horticultural practice of girdling branches. In one experiment, for instance, an average of nearly 1300 flowers were initiated in branches of larch which were girdled and tied down, compared with 400 in branches merely tied down. These results, and others, suggest that nutritional levels are important in respect to flowering.

There are thus a number of external or environmental factors which affect flowering of conifers. But even when external conditions are favourable to flower initiation, there remains the question of how it is that, for example, a 15-year-old larch tree initiates flowers but a five-year-old tree generally does not. It is clear that there must be internal factors influencing the onset of the reproductive phase in addition to environmental factors. In view of this, it is perhaps not surprising that, although two-year-old larch were in one experiment grown upside-down for a number of years, they did not form a single flower.

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OBITUARIES

Agnes Arber, F.R.S., F.L.S., died on 22 March 1960, in her eighty second year. Many visitors to Cambridge came to see Mrs Arber, as she was always known, in her house on Huntingdon Road. A little farther, now, may be their pilgrimage to Girton where she is buried with her husband E.A.N. Arber (d. 1918). For Mrs Arber's fame is world-wide. In her books, so finely illustrated by herself, the world discovered a great biologist and a great historian of botany, and from its four corners it came to talk. She was a recluse, but these visits delighted her, and much was it regretted that she could not enter more into the life of the nearby Botany School. No books in its library are so thumbed as hers, which revelation was a joy to her in her last months. The media which she inherited were the scholastic thought and the artistic line, and she will be read for many years to come because, though tersely to be styled a transverse-sectionalist, she excelled at recombining what had to be severed and in remounting it with consummate erudition on the escarpment of morphology. Dr H. Hamshaw Thomas has written of these works and of her career (*Nature* **186** (4278) : 847) and there is a gracious obituary in *The Times* (24 March 1960)*. She was elected a Fellow of the Linnean Society in 1908 and to the Fellowship of the Royal Society in 1946. She was awarded in 1948 the Linnean Gold Medal. To many she was the ' lady of botany ', and young biologists should think of an acute and powerful observer, wrapt in penetrating and ever more humane philosophy, who grasped the world without travel, and how they may attract into the circle of discussion such another if they are fortunate. The wind blew in gusts across the sunny field and mingled shouts of football with our thoughts at her grave. It was the laughter of her books. 'Lucem tuam Ovino da Deus et requiem '.

Sidney Fay Blake, F.L.S., who died suddenly on 31 December 1959, while at work at the Plant Industry Station of the U.S. Department of Agriculture in Beltsville, Maryland, was in his 67th year. He was born on 31 August 1892, in Stoughton, Massachusetts, a small town 18 miles south of Boston. From his early youth his chief interest was natural history, particularly ornithology. During his school years his interest in plants developed too, and in 1909, when he entered Harvard College he knew that he wished to be a botanist. Scholastically his college career (completed in three rather than the usual four years) was one of outstanding merit and he received his B.A. degree *summa cum laude* in addition to being elected to Phi Beta Kappa, the national honorary society for scholastic excellence, and to being awarded the honorary John Harvard fellowship. He was elected a fellow of the Society in 1951.

Dr. Blake was a modest man ; and although my acquaintance with him began some twenty years ago, during my early years of graduate study, I should not feel that I knew him so well had I not been privileged to read his letters for the years 1913–1918, to two of his professors, Dr Benjamin Lincoln Robinson, then Director of the Gray Herbarium, and Professor Merritt Lyndon Fernald, Fisher Professor of Natural History (Botany). During part of this time he held a Sheldon Travelling Fellowship from Harvard and wrote from England and the Continent of his experiences and his work. The outstanding characteristics to be observed in Blake's letters are the clarity with which he saw the direction of his career and the maturity of his thinking. He seems to have been not at all confounded by the doubts and uncertainties which beset most young graduate students, or by the complexities of the botanical problems he undertook. He was delighted with his life abroad and enjoyed tremendously his association with

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British and European colleagues. Although his work on the Continent was terminated in August 1914 by the outbreak of World War I, he continued his research at the British Museum until February, 1916, when he returned to the Gray Herbarium and completion of his graduate studies. In 1917 he received the Ph.D. degree at Harvard and at the end of that year began a long and useful career in the Department of Agriculture, which continued for forty-one years.

Blake published a tremendous number of botanical papers of highest excellence. Up to the time he left Harvard in 1917 he had more than seventy papers to his credit, including some of his best known studies in the Compositae (among them revisions of the genera *Encelia* and *Viguiera*), a family on which he became a recognized authority and in which his intense interest continued to his last years. He contributed treatments on Compositae and other families to many American floras and identified collections for many botanists. In all, he published more than three hundred botanical papers and numerous ornithological notes. Some twenty plants, as well as two fossil mollusca and a coral were named for him.

The work which occupied a large part of Dr Blake's time and effort for the last twenty years was the preparation of the *Geographical Guide to the Floras of the World*, a compendium of the most significant floristic studies. Part I of this work, compiled with the late Miss Alice C. Atwood, former librarian of the Department of Agriculture, and including references to America, Africa, and the islands of the Pacific, was published in 1942. Part II, covering western Europe, was in galley proof at the time of his death and is to be published in late 1960. Many aspects of this work were enormously tedious, but Blake continued it through the years with utmost care and precision. His working knowledge of many languages was a great asset, and his vast familiarity with details of European geography astonished even his European colleagues. The great respect in which Dr Blake was held by botanists throughout the world is made very clear in the large correspondence required for the preparation of the *Guide to the Floras* and by the great cooperation he received from those of whom he requested it. Without this aid even his tireless effort would not have sufficed to complete such a tremendous reference work, which will be used by his colleagues with gratitude for a long time.

Beyond those characteristics which led to his very numerous and excellent botanical achievements, recognized by even those who did not know him, Sidney Fay Blake had an engaging personality which endeared him to his associates. His quiet but very keen sense of humour, unusual alertness to his natural surroundings, and quick and active mind which he turned to many interests for his hours of pure pleasure were a joy to his companions. He was devoted to Sherlock Holmes and rather proud of his contributions to the *Baker Street Journal*. His kindness and generosity in helping his colleagues were unfailing. His simplicity and humility were steadfast.

Dr Blake is survived by his wife, Doris Holmes Blake, an entomologist, and a daughter, Doris B. Ullman.

BERNICE G. SCHUBERT.

Harry Howard Bloomer, F.L.S., was born on 28 October 1866 and lived in or near Birmingham until 1929, when he retired to Swanage; he died on 15 June 1960. His education was mostly of an elementary character that in after years necessitated much hard study. He qualified as a chartered accountant in 1893 and was taken into partnership in his firm, of which he became senior partner in 1900. After his final professional examination, he attended evening classes in geology at Mason College (afterwards Birmingham University) and the special biology course held on Saturdays. In later years he spent holidays at

Hornell's laboratory, Jersey, the Marine Biological Laboratory at Plymouth and the Liverpool Marine Biological Laboratory at Port Erin, Isle of Man.

In 1909 Prof. F. W. Gamble offered Bloomer a research table at the University of Birmingham, but owing to professional duties he was unable to make full use of it. He joined the Birmingham Natural History and Philosophical Society in 1894, being Treasurer for many years and President in 1927 ; he was also President of the Biological and Malacological sections. He was secretary of the Vesey Club, Sutton Coldfield, for a number of years. Bloomer was elected a member of the Malacological Society of London in 1898 and of the Conchological Society of Great Britain and Ireland in 1908, being President of the latter society in 1928. He also belonged to the British Ecological Society, the Marine Biological Association of Great Britain and the Botanical Society of the British Isles. He was nominated for fellowship of the Linnean Society by the President, Dr W. A. Herdman, and elected in 1907.

His health was never robust and in 1911 he made a voyage to Australia, where he met Hedley ; when in Queensland he spent much time with John Shirley botanizing and shell collecting. The following year he went to the Azores. Bloomer writes : ' Though I made a collection, mostly by purchase, of marine, land and freshwater shells, I am not in the true sense a collector, my interest is in the internal structure of the animal, its life history and its ecology. The greater part of the shells I gave to the Birmingham Museum on leaving Birmingham. Those of the Myacea I presented to the British Museum. The shells retained relate chiefly to my work on the freshwater bivalves of Great Britain, America and Africa. These have either been given to me or purchased, but I do not think they are of much value from a collector's point of view. My out-of-doors interests are gardening, walking, fly-fishing and botanizing. Since living in Swanage the migrant butterflies, the sea-birds and the passage to and fro of the migrant birds are a source of delight to me.'

Most of Bloomer's published papers concern the anatomy of bivalve Mollusca, marine and freshwater, though since 1917 his researches were virtually restricted to freshwater mussels (Naiades or Unionacea). Most of his papers appeared in the *Journal of Malacology* (to 1905), the *Proceedings of the Malacological Society of London* and the *Journal of Conchology*. He contributed two papers on the Scots Pine to the *Proceedings of the Birmingham Natural History and Philosophical Society* and was joint editor with W. B. Grove of *The Fauna and Flora of Sutton Park* (Birmingham Civic Society). Bloomer's collection of freshwater mussels has gone to the British Museum (Natural History). He was unmarried. This obituary has been compiled from notes left by Mr Bloomer and kindly placed at my disposal by Mr S. P. Dance.

Under his will Mr Bloomer left £500 to the Linnean Society, to be invested, and the income spent at the discretion of the Council.

A. E. Ellis.

William Ernest Dick, B.Sc., F.L.S. The sudden death of W. E. Dick on 12 January 1960, in his forty-sixth year, has ended prematurely the devoted work of a man, who, as the chief aim of his working life had set himself to build a bridge between the scientist and the non-scientist.

Dick was educated at King's School, Wimbledon, whence a state scholarship took him to the Imperial College. Ill-health, which dogged him for the rest of his life, compelled him to give up his scholarship. He became a journalist, and served with a number of provincial and national papers. When war began in 1939, he joined the A.F.S., but soon afterwards he was in France with the B.E.F. He was evacuated from Dunkirk, transferred to the R.E., and in 1941 was invalided out of the army. He returned to journalism, and soon became associated with *Discovery*. In 1945, he was appointed editor-in-charge, a spot he occupied until 1956. In the interval, he raised *Discovery* to its present eminent position, greatly increasing circulation, improving quality, and getting the magazine known all over the world. In 1956, he left *Discovery* to found a new periodical, *British Chemical Engineering*, and in 1958 he became editor of *Chemistry and Industry*, the journal of the Society of Chemistry and Industry.

In 1942, Dick joined part-time classes at Chelsea Polytechnic (now the Chelsea College of Science and Technology), and registered as an internal student of the University of London. He passed his subsidiary subject, zoology, in 1944, and completed his special degree in botany in 1945.

Dick was elected a Fellow of the Linnean Society in 1946. He often attended meetings, and, quite unobtrusively, served the society in a number of ways.

Dick was a firm friend, a good talker in congenial company and a deep thinker. Young men who were finding their way into science journalism and broadcasting could be sure of Dick's friendship ; he was always ready to go out of his way to advise them and help them in every way he could. He had his dislikes, but he was not a good hater, he did not bear malice, and he took knocks with quiet good humour. In particular he disliked pedantry, and what he called 'academic finicking'. He was a glutton for work, sparing himself not at all, and often working when he should have been resting. He had married in 1940, and his wife gave him much help in his busy life. In that life, he steadily pursued his master purpose, the faithful presentation of science to the layman. A thoughtful article, 'Science and the Press', printed in *Impact* (1954), may be taken as his confession of faith ; it may be considered as his chief contribution to the furtherance of a healthy development of organized science.

One idea he cherished seems, alas, unlikely to come to fruition. He was greatly interested in British flowering plants, many of which he grew in his garden. He talked often of a British flora with good coloured illustrations and with copious ecological and biological data, but he knew that such a book was not an economic proposition.

Dick wrote many general articles, and his monthly reports on the progress of science, based largely on information he had gathered personally from the workers concerned, were always a valuable feature of *Discovery*. With I. B. N. Evans, he wrote *Science and the Welfare of Mankind* (Simpkin Marshall, 1946), and he also wrote *The Story of Energy* (Bureau of Current Affairs, 1951), and *Atomic Energy in Agriculture* (Butterworth's, 1957).

B. BARNES.

Willem Marius Docters van Leeuwen was born in 1880 at Batavia in Java and educated at Amsterdam University where he took his Ph.D. in 1907.

His first post was as entomologist at the General Experimental Station at Salatiga in Java and the whole of his career, until his retirement, was in Indonesia. A man who showed great sympathy with the interest in the young, it was natural for him to teach. From 1909–15 he taught natural history at secondary schools at Samarang and later (1915–18) at Bandoeng. In 1918 he was appointed Director of the famous Botanic Gardens at Buitenzorg (now Bogor) and later held simultaneously a professorship at the Medical College, Batavia. After his retirement he became University Lecturer in Amsterdam and in 1942 he was appointed Professor.

These are, however, but the bare bones of his career, providing him with the means and opportunity for his life-long interest—ecology, and natural history in the field. For this the wide and unusual range of his knowledge, embracing birds and insects as well as plants, made him especially well equipped and his studies on the relations between ants and plants, in which he showed how the former act as agents both in seed and spore dispersal, were especially valuable. His work on galls (Zoocecidiae of the Netherlands Indies) is reckoned a classic.

His account of the mountain flora of the Pangrano-Gedeh volcano is of high merit as a description of a tropical mountain and its environment. He had a small hut at 3000 m. where he spent weeks alone making observations, and he is said to have climbed Pangrano more than 100 times. But of all his works he is probably best known for his excellent publications on the flora and fauna of Krakatau. All this work in the field necessitated lengthy absences from his office and brought him reprimands from his Ministry to which he replied that a tropical biologist should be a biologist and not a desk-worker.

His observations on flower biology in the Loranthaceae were particularly good and his work of a more formal taxonomic nature was by no means negligible.

Docters van Leeuwen was also an excellent photographer and his collection of photographs is preserved at Bogor where are also most of his herbarium specimens, numbering many thousands. His large collection of zoocecidia is, however, in the Leyden Herbarium.

Finally, those who knew him well, always record their memories of his congenial temperament and his unfailing encouragement to students who knew him as ' Uncle Doc '.

His wife, née Jenny Reynvaan who (with three children) survives him, also a biologist, was an immense help to him, especially in his work on galls, and his sister-in-law, née Catharina Carolina Reynvaan, who became his personal assistant at the Medical College, Batavia, made many collections with him and did much of the photography.

Docters van Leeuwen was elected Foreign Member of the Linnean Society in May 1939. He died on 25 February 1960.

Eric Marsden Marsden-Jones, F.L.S., F.R.E.S., was born at Tilston Rectory, near Malpas, Cheshire, on 8 May 1887, and was the only son of the Rev. Morris Jones. He was educated at Repton School but a serious accident when he was about 17 injured his spine and he spent several years on his back. Although he recovered sufficiently to be able to pursue his favourite studies in botany he suffered all his life from the effects of the injury. From his early school days he was interested in natural history and especially in botany. Marsden-Jones's first contact with controlled plant breeding was through Mr Hugh Aldersey of Aldersey Hall, who was a pioneer in sweet pea hybridization and selection. He made early contact with Prof. W. Bateson and the late Mr E. A. Bowles was also a close personal friend. In 1921 he married Miss Phyllis Dunn, who survives him. After a short period at Bournemouth he and his wife and mother settled at Potterne, near Devizes, Wiltshire, and it was there that the Potterne Biological Station was started in 1923. It occupied about two acres and was maintained till 1940.

The work at Potterne was mainly in three directions: the building up of a collection of British plants, genetical experiments, and transplant experiments. The collection of British plants was arranged systematically and was commenced in 1922 at Bournemouth. It grew to consist of over 800 herbaceous species from known localities. This living collection was kept in being by Marsden-Jones and his wife for many years and was used by numerous botanists. Since the material was carefully determined, constantly checked for contamination, localized from the wild, and made available freely to research workers, school or college students, and to botanical and agricultural institutions it was widely appreciated. Seeds were collected and seed lists distributed annually. In 1939 the collection was presented to Dauntsey School, Lavington, and is there used for teaching purposes.

The writer first met Marsden-Jones in 1924 and from then worked with him on the experimental taxonomy of various British plants and on the transplant experiments of the British Ecological Society. Work was concentrated on the British species of *Centaurea* and on the Bladder Campions (*Silene maritima* and *S. vulgaris*) but species of *Ranunculus* (including *R. ficaria*), *Saxifraga*, and *Anthyllis* were also investigated by field and herbarium studies and by numerous genetical experiments which involved the growing and scoring of many thousands of plants for numerous characters. A series of papers was published in the *Journal of Genetics*, the *Kew Bulletin*, and in other periodicals. The results of our researches on *Centaurea* appeared in a book *British Knapweeds*, Ray Society, London, 1954, and those on *Silene* in a second book *The Bladder Campions*, Ray Society, 1957. Accounts of the transplant experiments, in which 26 ramets of one clone of various species were grown on every one of five distinct soils at Potterne, with controls at Kew, appeared in the *Journal of Ecology* from 1930 to 1945. Marsden-Jones also investigated, in collaboration with the late Prof. F. E. Weiss, the genetics of flower colour in *Anagallis* and a summary of their work appeared in the *Proc. Linn. Soc.*, **171** : 27–29 (1960). He was always interested in the problems of pollination and accounts of his work with *Primula vulgaris* was published in the *Journ. Linn. Soc.*, **47** : 367–381 (1926) and of that on *Ranunculus ficaria* in op. cit., **50** : 39–55 (1935). A paper on the marble gall (*Adleria kollari*) was printed in the *Trans. Roy. Entomol. Soc., Lond.*, **104** : 195–222 (1953). Latterly he was investigating details of pollination in *Epilobium*, *Hedera*, and *Eupatorium* but his notes were left in too preliminary a condition for publication.

Series of voucher specimens of our joint researches, the index to the experiments, and a very fine series of samples mounted on cards have been presented to the Herbarium, Royal Botanic Gardens, Kew, the last through the Bentham Moxon Trustees.

Marsden-Jones was a very hard and conscientious worker. He was an excellent cultivator, but his interest was more in plants as individuals than in their arrangment in gardens. In experimental work he was meticulously careful and if anything was suspected by either of us of having gone wrong with an experiment it was scrapped and re-started. Similarly with the scoring, we had to agree on every point and doubts and uncertainties were considered again and again till an agreed decision was reached. Our relationships were always fully friendly and cordial and there was the fullest co-operation for over 35 years within the field of our joint researches, unmarred by any trace of a quarrel and with willing acknowledgment of what each contributed to the results.

E. M. Marsden-Jones was elected a fellow of the Linnean Society in 1914. He was also a fellow of the Royal Horticultural Society and served for many years on the Scientific Committee and Committee B, and a fellow of the Royal Entomological Society, as well as being a member of the Botanical Society of the British Isles, the Genetical Society, and the British Ecological Society. In October 1928 he was appointed by the Ministry of Agriculture and Fisheries Honorary Associate (Transplant and Breeding Experiments), Royal Botanic Gardens, Kew. He died in a nursing home in Bath on 26 August 1960.

W. B. TURRILL.

Henry Rissik Marshall was born on 17 May 1891 in the Transvaal. His family returned to Scotland in 1896 and he was educated at Marlborough and Trinity College, Oxford. He was a keen Territorial and served throughout the first World War and was at Gallipoli and later in Palestine. His marriage to the surviving daughter of Sir William Somerville, Professor of Rural Economy at Oxford, brought him into contact with his father-in-law's interests in botany, particularly in Alpine flora, so it was a keen pleasure to him when he was elected a Fellow of the Linnean Society in 1930. His sponsors included Somerville and Claridge Druce. His work (he became managing director of an investment company originally founded by his father) took him to several parts of South Africa and he had the opportunity of seeing much of the flora, and when he took up residence in London later, he coaxed many unusual plants to flourish in London soil. His other interests were shooting and fishing, and, above all, the collection of superb examples of early Worcester Porcelain, on which he wrote a book in 1954. The collection is now in the Ashmolean Museum.

Marshall presented a fine copy of ' illustrations of British Ornithology ' by Prideaux John Selby, a former Fellow, to the Society, hand coloured by two well-known Academicians of the day.

He died on 27 December 1959 at his house near Oxford, aged 68.

Thomas Archibald Sprague, D.Sc. The botanical world suffered a great loss when Dr T. A. Sprague, a well known botanist of international repute was removed from our midst at Cheltenham on the 22 October 1958.

Sprague was one of a large family. He was the son of Dr Thomas Bond Sprague and was born at Edinburgh on the 7 October 1877. He was educated at Edinburgh University where he was fortunate to be a student of the celebrated Professor Sir Isaac Bayley Balfour. Sprague inherited the love of natural history from both parents. After graduating B.Sc. with botanical distinction he spent one year (1898–1899) in South America collecting plants in botanically unexplored regions of Colombia and Venezuela.

On his return home he was appointed Assistant in the Herbarium, Royal Botanic Gardens, Kew. At that time work in the Herbarium was on a taxonomic basis, and Sprague was assigned the Polypetalae ; later when the work was divided on a geographical basis he was placed in charge of the South American collections. In addition Sprague specialized in various plant groups such as the Bignoniaceae, the Triumfettas of Africa, and in 1909 published a paper on these, jointly with Dr Hutchinson, in the Journal of the Linnean society. Sprague was also responsible for the difficult family Loranthaceae, accounts of which he prepared for the Floras of Tropical and South Africa. In this connection he visited several continental herbaria. Later for his paper (thesis) on the Adoxaceae he received the degree of Doctor of Science at Edinburgh University.

In the summer of 1913 Sprague, accompanied by Hutchinson, visited the Canary Islands where he collected in the little known island of La Palma. An account of this journey was published in Kew Bulletin 1913, No. 8.

For very many years Sprague was in charge of the Index Kewensis and supervised the publication of many of its Supplements. He discharged this responsibility with great zeal. Sprague also made an intensive study of the pre-Linnean Herbals for which he was specially qualified by reason of his knowledge of classical languages and his wide knowledge of botanical bibliography.

Sprague was also a recognized authority on plant nomenclature and was largely responsible for breaking away from the old " Kew Rule " and adopted wholeheartedly the International Rules. He took a leading part in many International Congresses and Conferences. At the International Congress held in Cambridge (England) in 1930, he acted as Recorder to the Nomenclature Section, in Amsterdam (1935) he was Rapporteur Général, and in Stockholm (1950) he was, jointly with Dr Merrill, President of the Section. He wrote numerous papers on various nomenclatural problems. In this connection he was most generous in freely giving aid and imparting his knowledge to the younger botanists. During the latter years of his service at Kew Sprague became Deputy Keeper of the Herbarium and Library and retired in 1945.

Sprague was possessed of a lively temperament, but his devotion to ideals, his unflinching courage in maintaining his convictions against all opposition, his abhorrence of any paltry action, must excuse a certain masterful manner, impatience, and contempt for hesitation in others in reaching conclusions. A somewhat irascible exterior often concealed a nature capable of great kindness to others by helping them with their botanical problems. He was capable of dropping work in hand to assist a young botanist with some knotty botanical problem. Many of the older members of the Kew Staff will remember with gratitude his kindly help and encouragement.

Sprague was not only an eminent botanist he was also deeply interested in Ceramics, and published several papers in *Apollo*. During one of his visits to Sweden he was shown Linnaeus's collection of porcelain (mainly Chinese) now housed in the Linnean Museum in Uppsala. He was most interested to see in this Linnean collection at least one prototype of an English specimen in his own collection.

Sprague was a Fellow of the Linnean Society since 1903, and served both on the Council and on the Library Committee.

H. S. A. MARSHALL.

Marie Charlotte Carmichael Stopes, D.Sc., Ph.D., who died on 2 October 1958, was elected a Fellow of the Linnean Society in 1909 and took a real interest in the Society until a short time before her death. She was the daughter of Henry Stopes, who gained distinction as an anthropologist, but died at an early age leaving a widow with two young daughters to educate. After a short period at St George's School Edinburgh, she entered the North London Collegiate School for Girls where the teaching of Natural Science was carried on with great success at that time.

From school she proceeded to University College London, where much interest was being taken in the newly discovered fossil plants from the palaeozoic rocks. In 1896 Dr D. H. Scott had given a course of lectures, later published as a book, *Studies in Fossil Botany*. The Head of the Department was Prof. F. W. Oliver who was actively engaged in palaeobotanical research and gave her much encouragement. She gained the distinction in her final examinations of a First Class and a Gold Medal in Botany. She next proceeded to the University of Munich where she spent two years of research under Goebel and Radelkofer. She was awarded the degree of Ph.D. for her thesis on the comparative structure of the seeds of Cycads and Pteridosperms. This work was important in connection with the recognition of the group of extinct plants which Oliver and Scott founded in 1902 under the name of Pteridospermae.

In 1904 Miss Stopes joined the staff of the botanical department of the University of Manchester. Here the pioneer work on the structure of fossil plants had been carried out by W. C. Williamson about a quarter of a century previously, and there was a fine collection of these fossils available. This petrified material was contained in calcareous concretions known as coal-balls, and an important study of the nature, distribution and origin of these concretions was undertaken in collaboration with Mr (later Professor) D. M. S.Watson. Somewhat similar concretions were known from Japan and in 1907 Miss Stopes went to Japan to collect this material. With the help of Prof. Fujii, she described her collections in an important paper, published by the Royal Society in which many new forms were described. This material proved to be of Cretaceous age and most of her subsequent research was on plants of this age.

In 1914 Miss Stopes was appointed Fellow and Lecturer in Palaeobotany at University College London. She made critical studies of the Cretaceous plants in the British Museum and produced two new volumes of the museum catalogues.

Of special interest were a group of specimens of petrified wood of Lower Cretaceous age which were probably derived from the earliest Angiosperms known at that time. (More recent studies on the comparative anatomy of woods shows that the structure of these specimens was of a more primitive type than was formerly believed.) In 1918 she published an account of the structure of two well preserved bennetitalean cones of considerable morphological interest.

During the War of 1914 she began work of much geological importance, on the structure of coal. She drew attention to the different constituents of coal, which were present in different relative amounts in different places and which determined the properties of the coal. The names she proposed for these constituents have been generally accepted. She published with Dr R. V. Wheeler an important monograph on the constitution of coal.

The last forty years of her life were largely devoted to social problems connected with family limitation. Her devoted work for the establishment of clinics, and for the education of the needy, has already had a wide-spread influence. She was twice married, first to Dr R. Ruggles Gates and after this marriage had been dissolved, to Mr H. Verdon Roe, the well known Aeronautical engineer.

H. HAMSHAW THOMAS.